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Life history and fisheries ecology of weakfish, Cynoscion regalis, in the Chesapeake Bay region

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Life history and fisheries ecology of weakfish, *Cynoscion regalis*, in the Chesapeake Bay region

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The College of William and Mary, 1994

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In Partial Fulfillment
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Doctor of Philosophy

By

Susan K. Lowerre-Barbieri

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This dissertation is submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

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ABSTRACT

Otoliths, scales, dorsal spines, and pectoral fin rays were compared to determine the best hardpart for ageing weakfish, *Cynoscion regalis*. Sectioned otoliths showed the clearest marks and were validated by the marginal increment method for ages 1-5. This validated method of ageing weakfish was then compared to the traditionally used scale method, which was found to be less-precise and to underage older fish. Ages of fish were consequently based on sectioned otoliths. Most weakfish from the Chesapeake Bay region were 200-600 mm TL and ages 1-4. Weakfish were not fully-recruited to commercial foodfish grades until age 2. Current maximum observed ages were age 12 in Chesapeake Bay and age 11 in Delaware Bay, although a fish collected in Delaware Bay in 1985 was age 17. Fish older than age 6 were rare in both areas. A probable range of total instantaneous mortality rates, based on a range of maximum ages (6-12), was 0.38-0.77. Although weakfish size was a poor predictor of growth, weakfish growth was well-described by the von Bertalanffy growth model (R^2=0.98, N=857). There was no evidence Delaware Bay weakfish reached a larger asymptotic length or size-at-age than Chesapeake Bay fish. However, maximum size and age fluctuated in Chesapeake and Delaware Bays over the past thirty years. Maximum size in both areas greatly increased from the late 1960's until roughly 1985, as did the numbers of large fish, apparently due to a series of strong year-classes, beginning in the late 1960's.

Weakfish are multiple spawners with indeterminate fecundity and a spawning season from May to August, in the Chesapeake Bay region. Sex ratios were approximately 3:1, females to males, in 1990-1992. Mean length at first maturity for males and females was 164 and 170 mm TL, respectively. Most fish were mature by age one and all fish were mature by age 2. Weakfish showed a strong diel periodicity, with almost all fish spawning at dusk. Most spawning females were 2- and 3-year-olds. Spawning activity was not consistent throughout the spawning season or between 1991 and 1992. Batch fecundities ranged from 75,289-517,845 eggs/female and significantly increased with both TL and somatic weight (P=0.0001). However, spawning frequency was higher in 1991 (every 2-3 days) than in 1992 (every 12-13 days), leading to an average annual fecundity of 7,369,750 eggs/females in 1991 and 1,808,056 eggs/female in 1992. Patterns of spawning activity within and between years appeared closely associated with feeding success.

Yield-per-recruit analysis indicated that, over a likely range of natural mortality rates, growth overfishing is currently occurring in the Chesapeake Bay region. Current t_c is $\leq$ age 2, whereas maximum yield consistently occurred at $t_c \geq$ age 6.

Life history and fisheries ecology of weakfish, *Cynoscion regalis*,

in the Chesapeake Bay region

GENERAL INTRODUCTION

Weakfish, Cynoscion regalis, is a recreationally and commercially important species found from eastern Florida to Massachusetts and, in times of high abundance, as far north as the Gulf of Maine (Bigelow and Welsh 1924, Bigelow and Schroeder 1953). It exhibits an inshore and northerly spring migration and an offshore and southerly fall migration, supporting fisheries in northern bays and sounds on a seasonal basis (Welsh and Breder 1923, Bigelow and Welsh 1924, Hildebrand and Cable 1934). In the Chesapeake Bay weakfish generally occur from April through November (Hildebrand and Schroeder 1928, Pearson 1941, Massmann et al. 1958), when they sustain one of the Bay's most economically important fisheries (Rothschild et al. 1981, Anon. 1984-1989).

North Carolina offshore waters are believed to be the major overwintering grounds, although younger fish (< 4 years) may stay closer to shore, and move further south (Pearson 1932, Wilk 1980). In spring, fish move into bays and estuaries along the coast to feed and spawn (Wilk 1979, Mercer 1985). Peak spawning has been reported to occur in May and June from South Carolina to Maryland (Nesbit 1954, Merriner 1973, Shepherd and Grimes 1984, Mercer 1985).

Several past studies concluded there were multiple

stocks of weakfish in the Middle Atlantic region based on: mark-recapture, meristics, morphometrics and regionally-specific growth and mortality (Nesbit 1954, Perlmutter et al. 1956, Seguin 1960, Shepherd and Grimes 1983). However, more recent studies have found no such stock structure (Crawford et al. 1988, Hawkins 1988, Graves et al. 1992) and suggest weakfish should be managed as a unit stock (Vaughan et al. 1991).

The question persists, however, as to whether weakfish demonstrate regionally different life history characteristics, which would greatly affect the proper management of this species. Weakfish age and growth have been reported to vary geographically, increasing with latitude (Pearson 1932, Nesbit 1954, Shepherd and Grimes 1983). Maximum reported age increases in a northerly direction: 12 years in New York (Shepherd and Grimes 1983), 9 years in Delaware (Seagraves 1981) and 6 years in North Carolina (Merriner 1973). Growth rates show a similar pattern (Shepherd and Grimes 1983). In addition, fecundity-at-length has been reported to decrease with latitude (Merriner 1973, Shepherd and Grimes 1984). However, it is unclear whether these differences are due to different population segments (Nesbit 1954, Perlmutter et al. 1956, Seguin 1960) or to the complex migrational pattern of one stock (Vaughan et al. 1991).

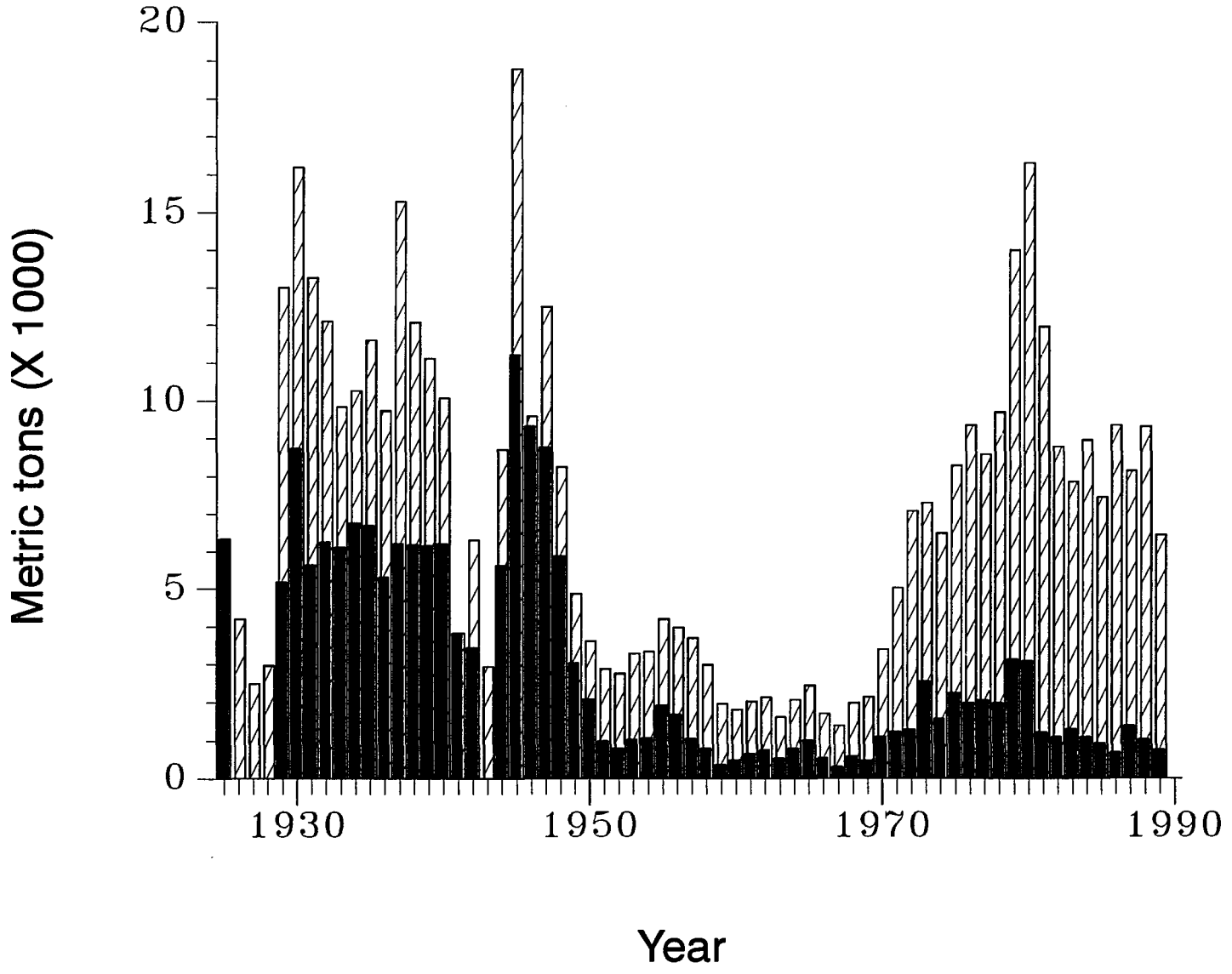
Historically, weakfish coastwide landings have greatly

fluctuated (Fig. 1). From 1940-1949 mean total landings were 8,800 metric tons (mt), peaking in 1945 with an annual catch of 18,800 mt (Shepherd and Grimes 1983, Mercer 1985). Catches declined during the period of 1950-1969 when mean annual landings were 2,600 mt. During the 1970's catches again rose with a mean annual landing of 7,700 mt (Crawford 1988). Landings peaked in 1980 at 16,300 mt (Boreman and Seagraves 1984, Mercer 1985), and in the past decade, mean annual landings have been approximately 8,000 mt/year (Anon. 1984 - 1989).

Regional contributions to total landings have also shifted in the past century (Joseph 1972, Merriner 1973, Mercer 1985). Prior to 1910 the Middle Atlantic region (New York, New Jersey, and Delaware) caught the most weakfish, peaking in 1908 with 11,600 mt (Merriner 1973, Mercer 1985). The Chesapeake region (Maryland and Virginia) took the lead from 1920 to 1950, reporting 11,230 mt in 1945 (Merriner 1973, Mercer 1985). Since 1958 the South Atlantic region (North Carolina, South Carolina, Georgia, and Florida), which is dominated by North Carolina, has landed the most weakfish. In 1980 South Atlantic catches reached 9,300 mt--more than all other regions combined (Mercer 1985).

Catch per unit effort (CPUE), with effort being measured as total counts of gear used, indicates coastwide CPUE peaked in 1945, declined through the 1950's, and increased from the 1960's to the mid-1980's (Mercer 1985).

Fig. 1. Commercial landings of weakfish coastwide (hatched bars) and in Chesapeake Bay (black bars), 1925-1989. Landings were not reported for the Chesapeake Bay region in 1926-1928 and 1943.


Metric tons (X 1000)
20
15
10
5
0
1930
1950
1970
1990
Year

The low levels of the 1950's and early 1960's have been accredited to: 1) overexploitation from 1945-1947 in the Chesapeake Bay, which harvested smaller fish than the middle Atlantic region (Perlmutter et al. 1956, Perlmutter 1959, Joseph 1972, Merriner 1973); 2) the effect of estuarine pollution on weakfish spawning and nursery grounds (Joseph 1972, Mercer 1985); and 3) an increase in gear efficiency from 1930-1955, allowing greater rates of exploitation, as gear use shifted from predominately stationary to more mobile gear (Perlmutter 1959).

Increased landings and CPUE from the late 1960's to the mid-1980's are harder to explain, and indicate a better measurement of effort is necessary (Joseph 1972, Rothschild et al. 1981, Mercer 1985). It was during this same time period that the recreational fishery greatly expanded (Merriner 1973, Wilk 1979, Mercer 1985), even higher numbers of small fish were being harvested in North Carolina (Merriner 1973, Mercer 1985), and a large number of weakfish were being caught as by-catch in the South Atlantic shrimp fishery (Merriner 1973, Wolff (1972) as cited in Mercer 1985).

Management of this species has been by individual states, regulations primarily consisting of size limits and occasionally gear restrictions (Mercer 1985). In 1985, the Atlantic States Marine Fisheries Commission (ASMFC) issued a management plan calling for interstate cooperation in the

collection of biological and fisheries data, on which management models could be built. It stressed the need for better understanding of weakfish migrations, reproduction, age composition and mortality.

Any management plan will have to incorporate regional differences in population parameters, as well as coast-wide fishing pressure. The Chesapeake Bay is an important area for weakfish in terms of its fishery and as a spawning and nursery ground (Joseph 1972, Chao and Musick 1977, Merriner 1973, Olney 1983, Cowan and Birdsong 1985), yet current regional population parameters have not been estimated. The objectives of this research are to determine age and growth parameters, reproductive pattern and fecundity, and mortality for weakfish in the Chesapeake Bay, and to use these parameters in yield-per-recruit models to determine the best management strategy.

CHAPTER 1

A comparison of age determination methods for weakfish

INTRODUCTION

Weakfish age and growth studies have been based almost exclusively on scales (Taylor 1916, Nesbit 1954, Perlmutter et al. 1956, Massmann 1963a, Merriner 1973, Shepherd & Grimes 1983). However, problems with this method have been reported: (1) small fish may not lay down a first annulus on scales (Welsh & Breder 1923); (2) older fish have closely-spaced annuli, which are hard to interpret (Taylor 1916, Shepherd 1988); (3) annuli form over a long time period, April-August, and scales are difficult to interpret during annulus formation (Nesbit 1954, Massmann 1963b); (4) there is annual and regional variation in the time annuli form (Perlmutter et al. 1956); and (5) checks or false annuli, and regenerated scales are common (Merriner 1973). The scale method of ageing weakfish also has not been conclusively validated by current standards (Beamish & McFarlane 1983, Brothers 1983). Perlmutter et al. (1956) and Shepherd & Grimes (1983) both tried to validate annuli on scales by the marginal increment method, however they used pooled age data and did not report the age range.

Although recent studies have shown that for many

species the scale method underages older fish at the point where fish growth becomes asymptotic (Beamish & Chilton 1981, Beamish & McFarlane 1983, Barnes & Power 1984), there has been little evaluation of other weakfish hardparts. Merriner (1973) compared weakfish scales to whole vertebrae and otoliths, and Villoso (1989) compared whole otoliths to scales, both concluding scales were best. However, Merriner's study was conducted before thin-sectioning of otoliths (Williams & Bedford 1974, Beamish 1979, Beamish and Chilton 1981) and other hardparts became common and Villoso (1989) did not consider thin-sectioning.

A decline in weakfish landings since 1980, coupled with greater competition between fisheries, caused the Atlantic States Marine Fisheries Commission (ASMFC) to develop a weakfish management plan in 1985 (Mercer 1985). Since then the ASMFC has issued an updated stock assessment (Vaughan et al. 1991) and suggested a 25% reduction in coast-wide exploitation rates (Amendment No. 1 of the Weakfish Fishery Management Plan of the ASMFC). However, it is essential to proper weakfish management that a validated, ageing technique be developed and used, as improper ageing can lead to faulty estimates of model parameters such as age at maturity, growth, longevity and mortality (Beamish & McFarlane 1983).

The objectives of this study were to: (1) compare otolith, dorsal fin spine and pectoral fin ray sections,

with scales in terms of: legibility and interpretation of potential annual marks, ease of collection and processing, and precision; (2) validate the hardpart demonstrating the greatest clarity by marginal increment analysis for each age group found in the Chesapeake Bay area; and (3) conduct a more in-depth comparison of the validated hardpart with scales, in terms of: precision and accuracy, time of annulus formation, growth estimates and use in back-calculation of body length.

MATERIAL AND METHODS

Preliminary comparison of hardparts

Four hundred weakfish were collected every other week during April-October in 1989 from three Chesapeake Bay commercial pound-nets. On each collection day, one 22.7 Kg (50 lb) box of each available grade of weakfish—small, medium, or large—was bought and all fish within it processed. Fish were measured for total length (TL ± 1.0 mm), sexed, and both sagittal otoliths were removed and stored dry. Scales were removed from an area just posterior to the tip of the left pectoral fin, below the lateral line. The left pectoral fin and the entire dorsal fin were removed by cutting below the base of the rays. Scales and fins were stored in paper envelopes and kept frozen until preparation for ageing.

A total of 45 fish, 15 from each grade, were randomly selected from the fish collected in 1989 for a preliminary comparison of hardparts. These fish ranged in total length from 244 to 615 mm and each of their four hardparts was prepared for reading as described below.

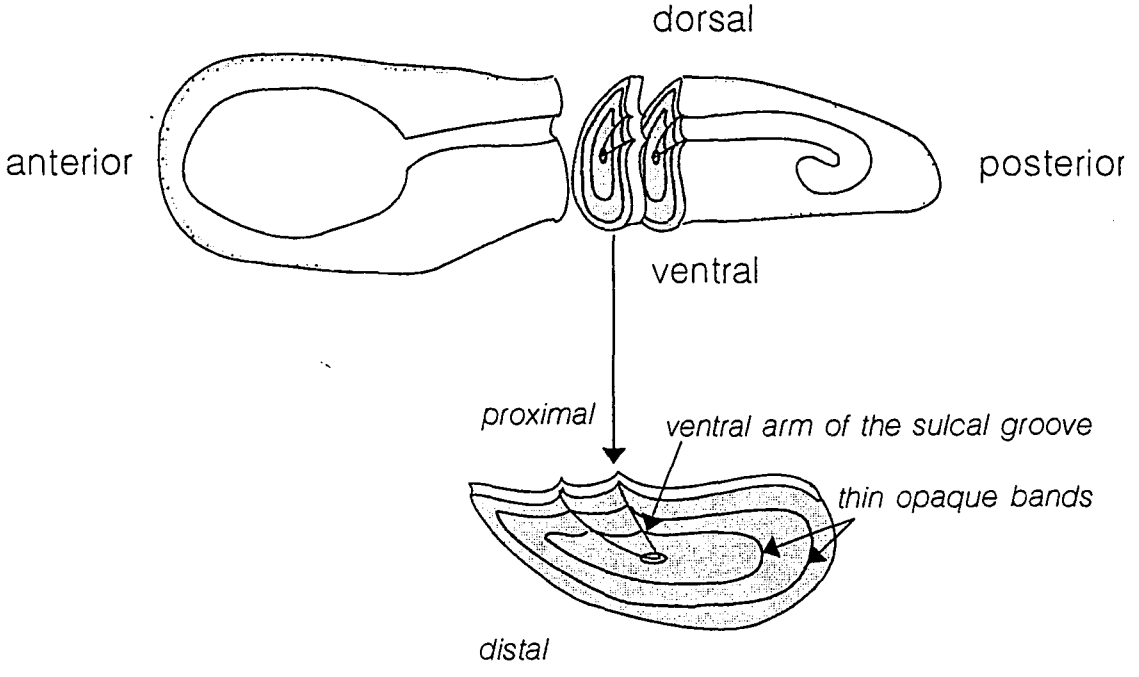
The right otolith from each fish was transversely

sectioned through the nucleus with a Buehler low-speed Isomet saw. Sections, 350-500 μm thick, were mounted on glass slides with Flo-Texx clear mounting medium and viewed under a dissecting microscope at 24x magnification using transmitted light and bright field, with the exception of samples from the period April-May, when sections were also read with reflected light and dark field to help identify the last annulus. Thin opaque bands, presumed to represent annual marks, were counted along the otolith sulcal groove (Fig. 2). Because opaque bands inhibit light passage, they appeared dark in transmitted light (Fig. 3a) and light in reflected light.

Scales from each fish were soaked in water until soft, after which they were washed gently using a soft-bristled tooth brush. Three or four clean, unregenerated scales were then dried, taped to an acetate sheet, inserted between two other blank sheets, and pressed with a Carver laboratory scale press for 2 minutes at 2,721 kg of pressure and 71^0 F. Due to the large size of weakfish scales, scale impressions were read using a standard microfiche reader at 20x. Those scales with potential annuli crowded along the scale periphery were also viewed at 48x under a dissecting microscope. Presumed annual marks were identified by standard criteria (Bagenal & Tesch 1978, Shepherd 1988).

One spiny ray from the dorsal fin and one soft ray of the left pectoral fin were prepared from each fish. Rays

Fig. 2. Schematic representation of a transverse section taken through the right sagittal otolith. The ventral arm of the sulcal groove, along which otoliths were measured, is indicated. The whole otolith is positioned as it would be in a weakfish.


dorsal
anterior
posterior
ventral
proximal
ventral arm of the sulcal groove
thin opaque bands
distal

were serially sectioned, starting at the base and through most of their length, at a thickness of 400 μm using a Buehler low-speed Isomet saw. Sections were then mounted on microscope slides with Flo-Texx and read under a dissecting microscope using transmitted light with dark field at 64x. Presumed annual marks were counted where they could be identified as individual, opaque bands.

Each hardpart was read twice by two separate readers. Readings were done in a randomly selected order, with no knowledge of collection date or fish size. Hardparts were evaluated in terms of clarity of presumed annual marks, ease of collection and processing, and precision. Precision was measured by average percent agreement within and between readers, i.e., percent agreement within readers was calculated for each reader separately and then averaged for the two readers and percent agreement between readers was calculated separately for each reading and then averaged for the two readings.

Validation of the otolith method

Because otoliths were found best for ageing, additional samples were collected for validation. During 1989-1992, 1,928 weakfish were collected from commercial pound-net, haul-seine, and gill-net fisheries in Chesapeake Bay. During March-November when weakfish do not occur in the

Chesapeake Bay, fish were collected (N=289) from the trawl fishery operating in North Carolina shelf waters north of Cape Hatteras.

The marginal increment method was used to validate otolith annuli (Brothers 1983, Casselman 1987, Hyndes et al. 1992). The translucent margin outside the proximal end of the last annulus was measured along the ventral side of the otolith sulcal groove (Fig. 2). Measurements were taken with an ocular micrometer to the nearest 0.038 mm (one micrometer unit at a total magnification of 24x).

Comparison of scales and otoliths

To compare the otolith and scale methods in more detail, 155 fish ranging from 140 to 845 mm TL were selected by stratified, random subsampling—strata being otolith-determined ages—from a total of 300 fish collected in 1989 and 1992. Thirty fish were selected from each of the age-strata, 1-4. Because older fish were scarce, only 14 age 5, 16 age 6, two age 7, two age 8, and one ten-year-old were included. Although most fish came from Chesapeake Bay commercial fisheries, to increase the number of older fish, 27 fish were collected in May 1992 at the Delaware Bay Weakfish Sport Fishing Tournament. I collected an additional 20 fish in August 1992 to include fish from each of the summer months for marginal increment and back-calculation analyses.

Hardparts were prepared as described for the preliminary comparison and read twice by each of two readers. An effort was made to determine annuli on scales based only on physical criteria and not to assign annuli based on any preconceived ideas of growth (Casselman 1983). Reading order was randomized and collection date and fish size were unknown. Each reader recorded the number of presumed annuli and a "+" if there was growth beyond the last annulus or a "*" if the last presumed annulus was forming or had just formed (Casselman 1987). After all hardparts had been read, ages were assigned using a January 1 birthdate, knowledge of the time of annulus formation, the relative growth of the hardpart margin and date of capture.

Variability within reader, between readers and between hardparts was analyzed by percent agreement. When an individual reader's counts of presumed annuli disagreed, a third reading was made as a tie-breaker. When readers ages disagreed, a third reading with both readers was made to resolve the disagreement.

To compare time of annulus formation and its variability in scales and otoliths, mean monthly relative marginal increments and their ranges were calculated and plotted (April-October). Relative marginal increments were calculated by dividing the marginal increment by the hardpart radius. All ages were pooled. Additionally, those hardparts which had been designated as having an annulus on

the margin ("*") were reviewed and their time of collection recorded.

To determine marginal increments and to conduct back-calculation analyses, hardparts were measured using a Via 100 camera/monitor system with a dissecting microscope at 24x. Otolith radius (OR) and otolith annular radius (OAR)—the distance from the nucleus to the proximal edge of each annulus—were measured along the ventral arm of the sulcal groove. Scale radius (SR) and scale annular radius (SAR) were measured along the left radius (Ricker 1992). Marginal growth was measured from outside the last annulus to the hardpart edge.

To evaluate the applicability of scales and otoliths for back-calculation, it was necessary to first analyze separately their total length to hardpart relationships. Seasonal effects were assessed by comparing hardpart size of one age class taken from different seasons to that predicted by the linear regression of total length on hardpart size for all fish. Only one age class (age 3) was used to remove any confounding effects of age. This age class was chosen because it was well-represented throughout the seasons.

Back-calculation relationships for both scales and otoliths were based on the "body proportional" hypothesis (Francis 1990) proposed by Whitney and Carlander (1956):

$$L_i = [g(S_i)/g(S_c)]L_c$$

where g is the total length on hardpart radius function, L_i

is back-calculated TL at age i, S_i is the measured hardpart size at annulus i, and S_c and L_c are the respective hardpart size and total length at capture. Only fish collected in April and May—the beginning of the somatic growth season—were used, to remove seasonal effects from the back-calculation equations (Ricker 1992). Because body-proportional back-calculation is based not just on the relationship of hardpart size to total length, but also on the relationship of hardpart size to consecutive annuli, mean annual growth increments were also calculated and compared between scales and otoliths.

The tendency for older fish to produce smaller back-calculated lengths-at-younger ages than observed, known as Lee's phenomenon (Smith 1983), was evaluated by calculating mean scale annular radii (SAR) and mean otolith annular radii (OAR) for each age at capture. In this way it was possible to determine if older fish demonstrated slower hardpart growth at younger ages, or true Lee's phenomenon, as opposed to calculation error (Smale and Taylor 1987).

Data were analyzed using χ^2 tests and regression methods available through the Statistical Analysis System (SAS 1988). Rejection of the null hypothesis in statistical tests was based on α=0.05. Assumptions of linear models were checked by residual plots as described in Draper & Smith (1981).

RESULTS

Preliminary comparison of hardparts

All four hardparts showed concentric marks that were interpreted as annuli (Fig. 3). However, marks on the dorsal spines and pectoral rays were inconsistent, often blurred or impossible to follow around most of the section and difficult to interpret. Presumed annuli on scales were distinctly clearer and more regular than those on dorsal spines and pectoral rays, but they still required some subjective interpretation. Presumed annuli on otoliths were exceptionally clear, consistent and easy to interpret.

Typical otolith sections showed an opaque nucleus, surrounded by a translucent zone, followed by a pattern of thin opaque zones alternating with wide translucent zones along the sulcal groove (Fig. 3a). In some sections the translucent zone between the nucleus and the first opaque zone was relatively small and made more opaque by a number of fine, circular, opaque bands. However, in all sections the first opaque zone beyond the nucleus was easily identified and considered to be the first annulus. Otolith marks were invariably clear, easy to identify and could be

Fig. 3. Marks on hardparts taken from a 2-year-old (as aged by otoliths) female weakfish, total length=392 mm collected in mid-September. (a) otolith section, as seen in transmitted light, bar=1 mm; (b) pectoral ray section, as seen in reflected light, bar=0.5 mm; (c) dorsal spine section, as seen in reflected light, bar=0.5 mm and d) scale impression, as seen in transmitted light, bar=1 mm. The left radius, which was the scale measuring axis, is marked. Ch=check. Arrows indicate individual marks counted.

a
b
c
d
Ch

interpreted with confidence.

Presumed annuli on scales were harder to identify than those on otoliths, but were usually identifiable as a clear zone in the anterior field where circuli were either absent or more widely spaced and by cutting over in the lateral fields (Fig. 3d). Checks did occur and they were most apparent in the anterior field. A clear zone in the anterior field was considered a check if it was not accompanied by distinct cutting over in the lateral fields. The first annulus was the hardest to identify. It rarely showed a clear band in the radii zone, although cutting over was sometimes apparent. Its position was based predominantly on the first point at which a large number of secondary radii originated.

Presumed annual marks on dorsal spines were fairly clear in some sections, but incomplete or blurred in others (Fig. 3c). Pectoral-fin ray sections were consistently hard to interpret (Fig. 3b). Presumed annual marks on both these hardparts appeared as wide, opaque, semicircular bands alternating with narrow translucent zones.

Otoliths showed the greatest precision, with 100% average agreement within and between readers. Scales also had high average agreement: 89% within readers and 80% between readers. Dorsal and pectoral fin sections showed the lowest agreement (Table 1) and little confidence was attached to their age assignments.

Table 1. Average percent agreement in the preliminary comparison of weakfish hardpart mark counts within readers, between readers and with otoliths.

Hardpart	Within readers	Between readers	With otoliths
Scales	89	80	27
Pectoral rays	59	64	49
Dorsal spines	66	76	46
Otoliths	100	100	

The number of presumed annual marks on otolith sections agreed poorly with those on other hardparts (Fig. 4). Scale and otolith readings agreed only 27% of the time (Table 1) and scales consistently had one less mark than otoliths (26 out of 45). Pectoral and dorsal rays showed better agreement with otoliths than scales, 49% and 46% respectively.

Validation of the otolith method

Opaque bands are laid down on otoliths once a year in the spring. Mean monthly marginal increment plots for ages 1-6 showed only one trough during the year, indicating only one opaque band was formed per year (Fig. 5). A few fish began to lay down annuli in March, as shown by the decrease in mean marginal increment and a relatively high variation in marginal increment size. However, lowest marginal increment values occurred in April and May, indicating most fish formed annuli during these months. Greatest otolith growth occurred during the months of June, July, August and September, as demonstrated by the step-wise increase in mean marginal increments. By October, mean marginal increments reached a fairly stable maximum, indicating little or no otolith growth. This maximum continued until the next March or April, when annuli were again laid down.

Due to the scarcity of older fish, it was not possible to conclusively validate fish older than age 5 by separate

Fig. 4. Counts of presumed annuli from weakfish scales, pectorals and dorsals compared to otoliths. The number of fish each point represents is indicated. The 45^0 line represents 100% agreement.

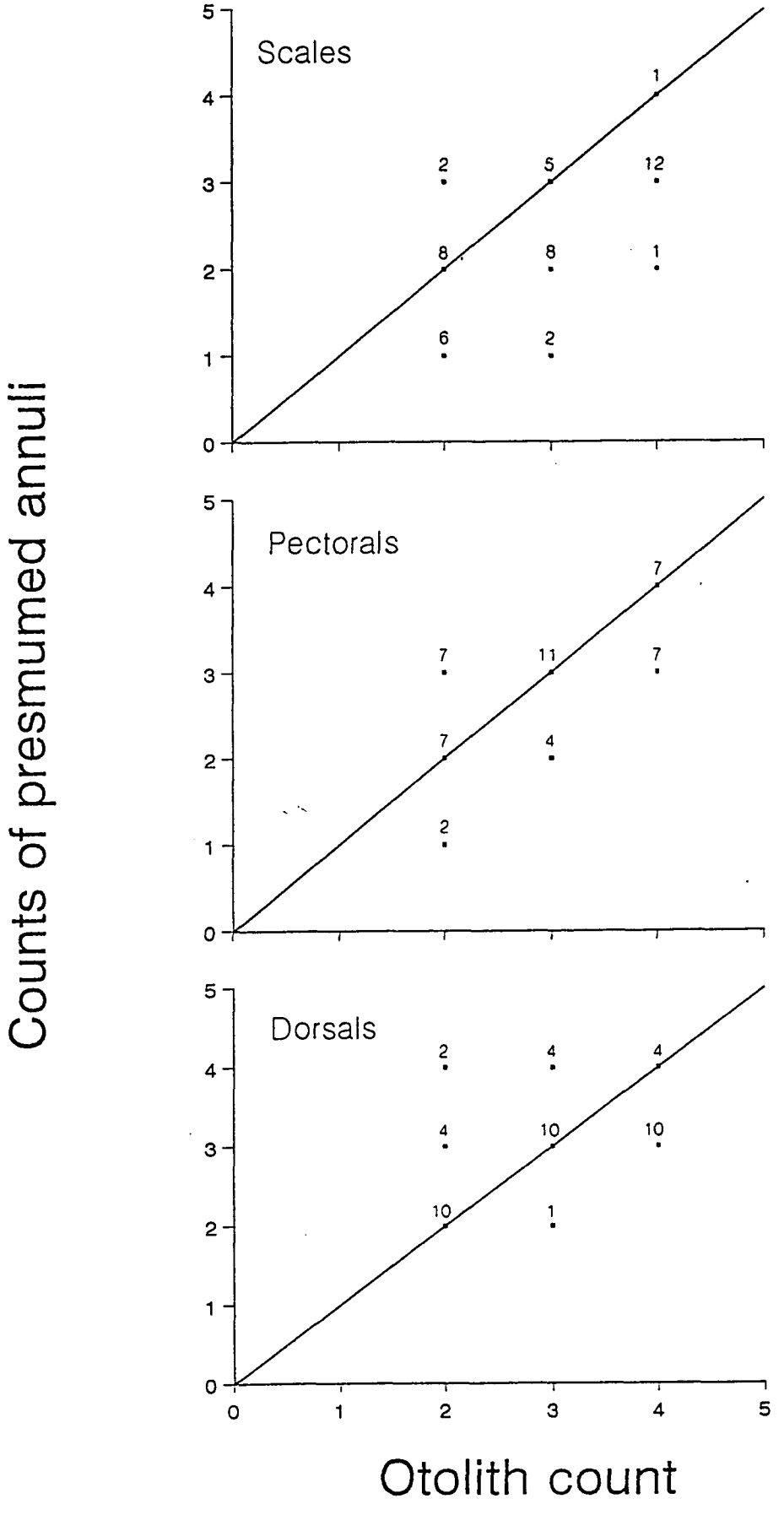
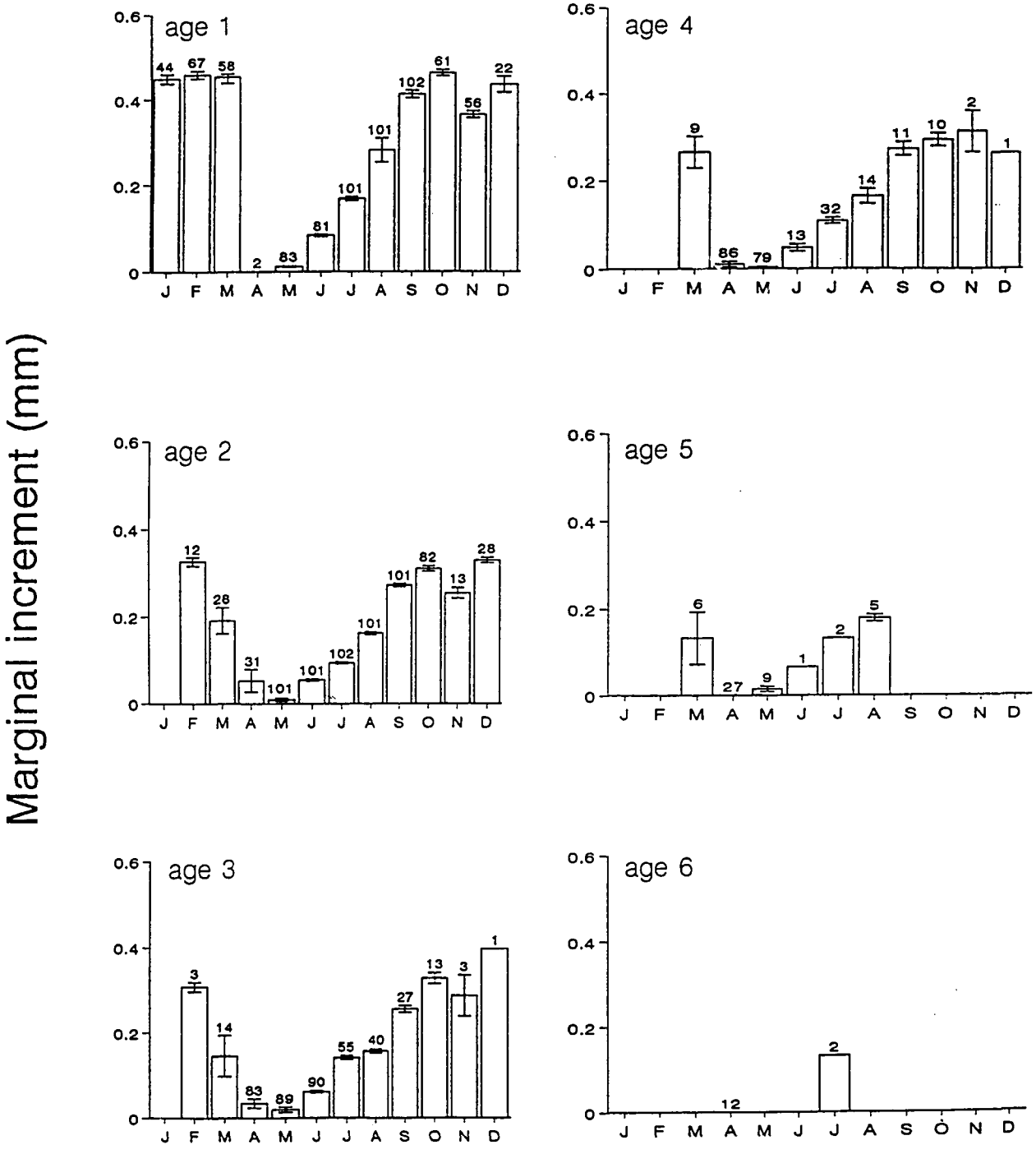

Scales
Pectorals
Dorsals
Counts of presumed annuli
Otolith count
0
1
2
3
4
5

Fig. 5. Mean monthly otolith marginal increments for weakfish, pooled over ages, 1-6, and years, 1989-1991. Vertical bars are ± one standard error. Numbers above the bars represent sample size.


age 1
0.6
0.4
0.2
0
44 67 58 2 83 81 101 101 102 61 56 22
J F M A M J J A S O N D
age 4
0.6
0.4
0.2
0
9 86 79 13 32 14 11 10 2 1
J F M A M J J A S O N D
age 2
0.6
0.4
0.2
0
12 28 31 101 101 102 101 101 82 13 28
J F M A M J J A S O N D
age 5
0.6
0.4
0.2
0
6 27 9 1 2 5
J F M A M J J A S O N D
age 3
0.6
0.4
0.2
0
3 14 83 89 90 55 40 27 13 3 1
J F M A M J J A S O N D
age 6
0.6
0.4
0.2
0
12 2
J F M A M J J A S O N D
Marginal increment (mm)
Month

marginal increment plots. However, there was no evidence that the pattern of annulus formation changed within the weakfish lifespan. Annuli were consistently formed during March-May for fish of different sizes, sexes and ages (1-6), and otoliths did not form more than one mark per year, even though these ages represented various stages in the fish's life history. Additionally, of the 2,217 otoliths examined (ages 1-10), all those in the process of forming or which had just formed annuli were collected in March-May. Thus, I assumed for ages 1-10, that the otolith method provided accurate ages.

Comparison of scales and otoliths

Scales were consistently more difficult to read than otoliths, and confidence in scale readings was often low. Percent agreement within and between readers was fairly consistent for both hardparts. However, otoliths showed much higher agreement: 98-100%, than scales: 78-80% (Table 2).

Although agreement between scales and otoliths was fairly high, 79%, agreement decreased with increasing age. Of 32 disagreements, only 6 differed by more than one year (Fig. 6). However, 4 of the 5 fish older than age 6 were underaged by scales and two of the oldest fish, age 10 and 8, were underaged by 3 years. Scales from older fish, if they showed more than 6 annuli, had marks which were

Table 2. Percent agreement of weakfish scale- and otolith-assigned ages within readers, between readers and between hardparts.

Hardpart	Within reader 1	Within reader 2	Between readers	With otoliths
Scales	80	78	80	79
Otoliths	100	98	99	

severely crowded and fragmented, even when viewed at higher magnification (Fig. 7a), whereas otoliths from these same fish showed clear annuli (Fig. 7b).

Although the number of fish underaged was small, their effect on estimating growth curves would be dramatic. Mean body size-at-age based on scales, although slightly curvilinear, showed no clear indication of an asymptote (Fig. 8a) and thus would not be appropriate for fitting a von Bertalanffy growth curve (Gallucci & Quinn 1979). In contrast, mean body size-at-age based on otoliths showed the clear beginnings of an asymptote (Fig. 8b).

Although sex of the fish had no effect on the precision or repeatability of scale readings, it did affect accuracy. Agreement of scale ages among and between readers was quite similar when calculated separately by sex, ranging from 75.0-79.5%. However, agreement between scale and otolith ages, or accuracy, was significantly different for males and females (χ^2=6.25, N=154, P<0.05). Of the 32 discrepancies between scale and otolith ages, 26 were males. Even if the fish greater than age 6 are discounted, there is still a significant difference (χ^2=5.79, N=149, P<0.05).

Time of annulus formation is not the same for scales and otoliths. Both hardparts showed only one trough in their mean monthly marginal increments (Fig. 9). However, otoliths with annuli on their margins were collected only during a discrete time period—April 1 through June 1—while

Fig. 6. Weakfish assigned ages from scales and otoliths. The number of fish each point represents is indicated. The 45^0 line represents 100% agreement.

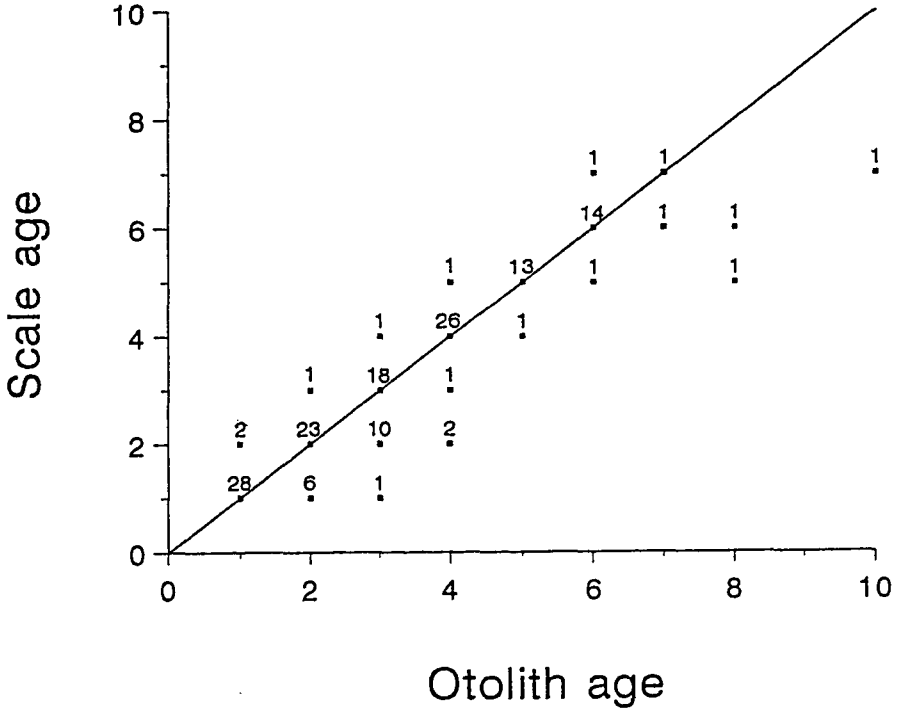

Scale age
Otolith age
0
2
4
6
8
10
28
2
23
1
6
18
1
10
1
26
1
2
1
13
1
1
14
1
1
1
1
1
1

Fig. 7. The scale impression (a) and sectioned otolith (b), as seen in transmitted light, from a male, 10-year-old weakfish, total length=845 mm, collected in mid-May. Arrows indicate marks counted as annuli.


a

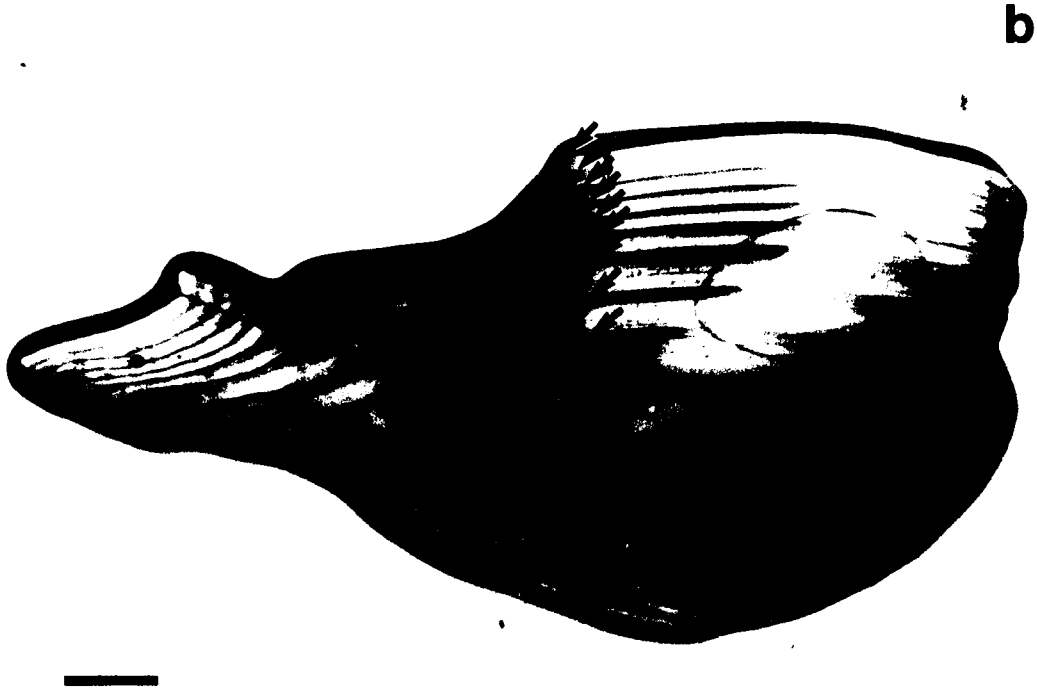
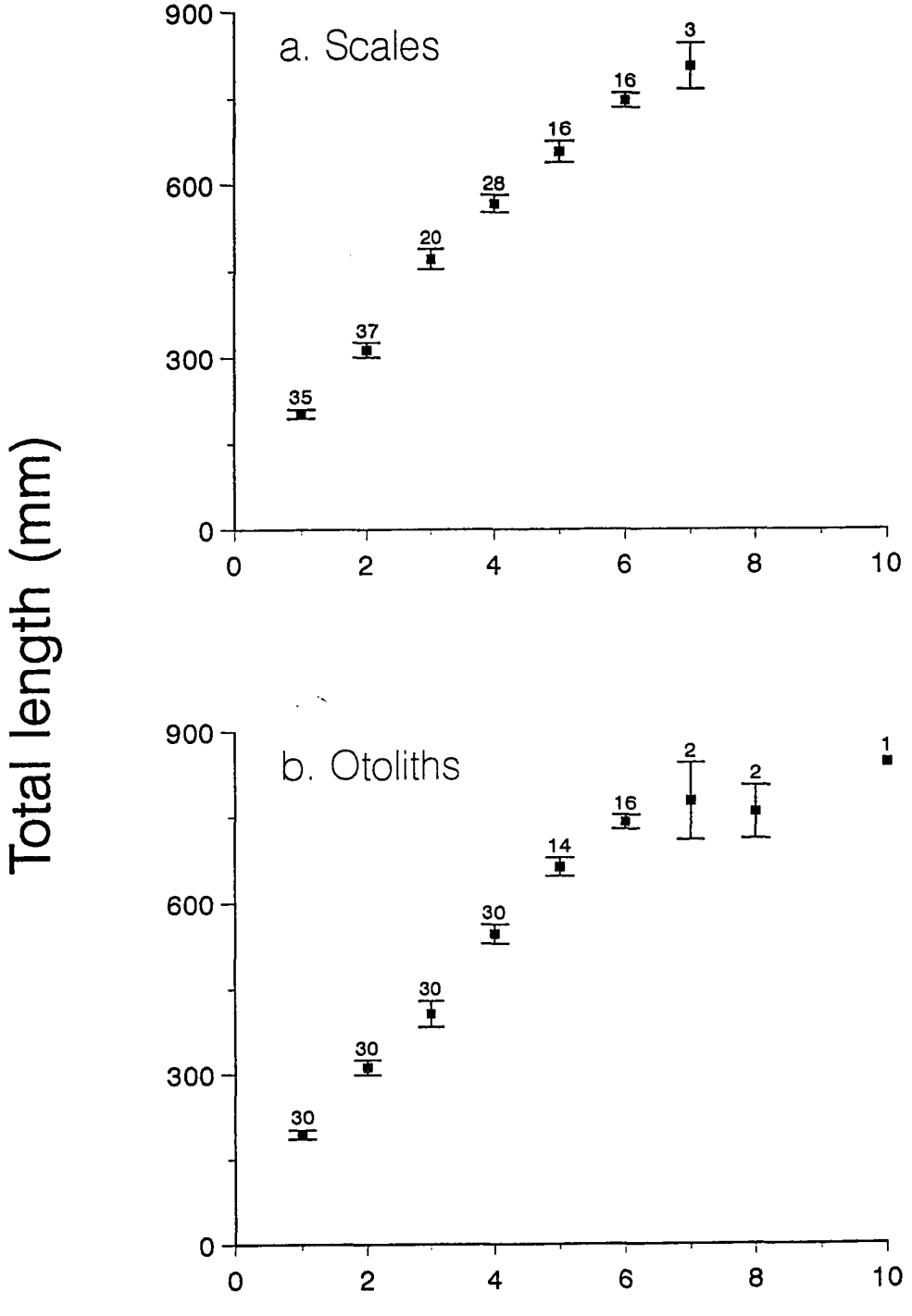

b

Fig. 8. Mean weakfish size at age: (a) based on scales and (b) based on otoliths. Vertical bars are ± one standard error. Numbers above the bars represent sample size.


a. Scales
b. Otoliths
Total length (mm)
Age (years)
900
600
300
0
0
2
4
6
8
10
35
37
20
28
16
16
3
30
30
30
30
14
16
2
2
1

scales in the process of forming annuli were collected from mid-April to mid-August, although most scales formed annuli in August. The variable and extended time of scale annulus formation is represented by the shallow trough (Brothers 1983) and the larger standard errors of the scale marginal increment plot, as compared to that of otoliths (Fig. 9).

Although total length on hardpart size relationships for both scales and otoliths showed linear trends (R^2=0.94 and 0.88 respectively, N=175, P=0.0001), the total length on otolith relationship showed seasonal variation. When a single age class (age 3) was marked by season of collection and plotted against the linear relationship predicted by the total sample (Fig. 10), all fish collected in April and May had smaller than predicted otolith radii, while fish collected in August and September had larger than predicted radii. Fish collected in June and July were intermediate, although most of their radii were also smaller than predicted. Scales from the same fish did not show similar seasonal trends.

Back-calculation equations of total length on hard-part size were calculated only for fish collected at the beginning of the growing season, in April and May, to remove seasonal effects. Although linear regressions were significant for scales (R^2=0.95, P=0.0001) and otoliths (R^2=0.92, P=0.0001), a quadratic term improved the model fit and was significant (P=0.0003 scales, P=0.0001 otoliths)

Fig. 9. Mean monthly relative increments for weakfish scales and otoliths. Vertical bars are ± one standard error. Numbers above the bars represent sample sizes.

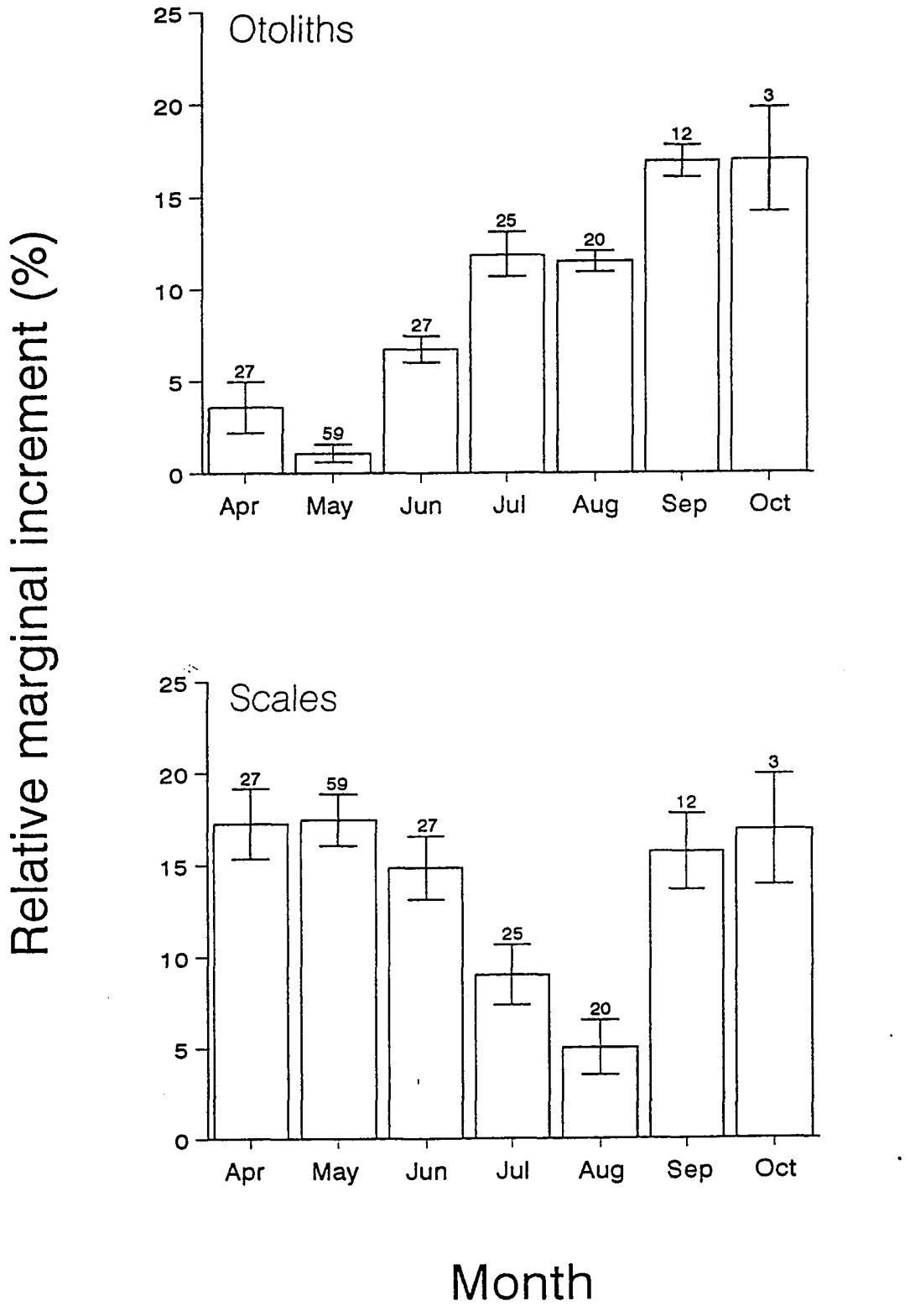
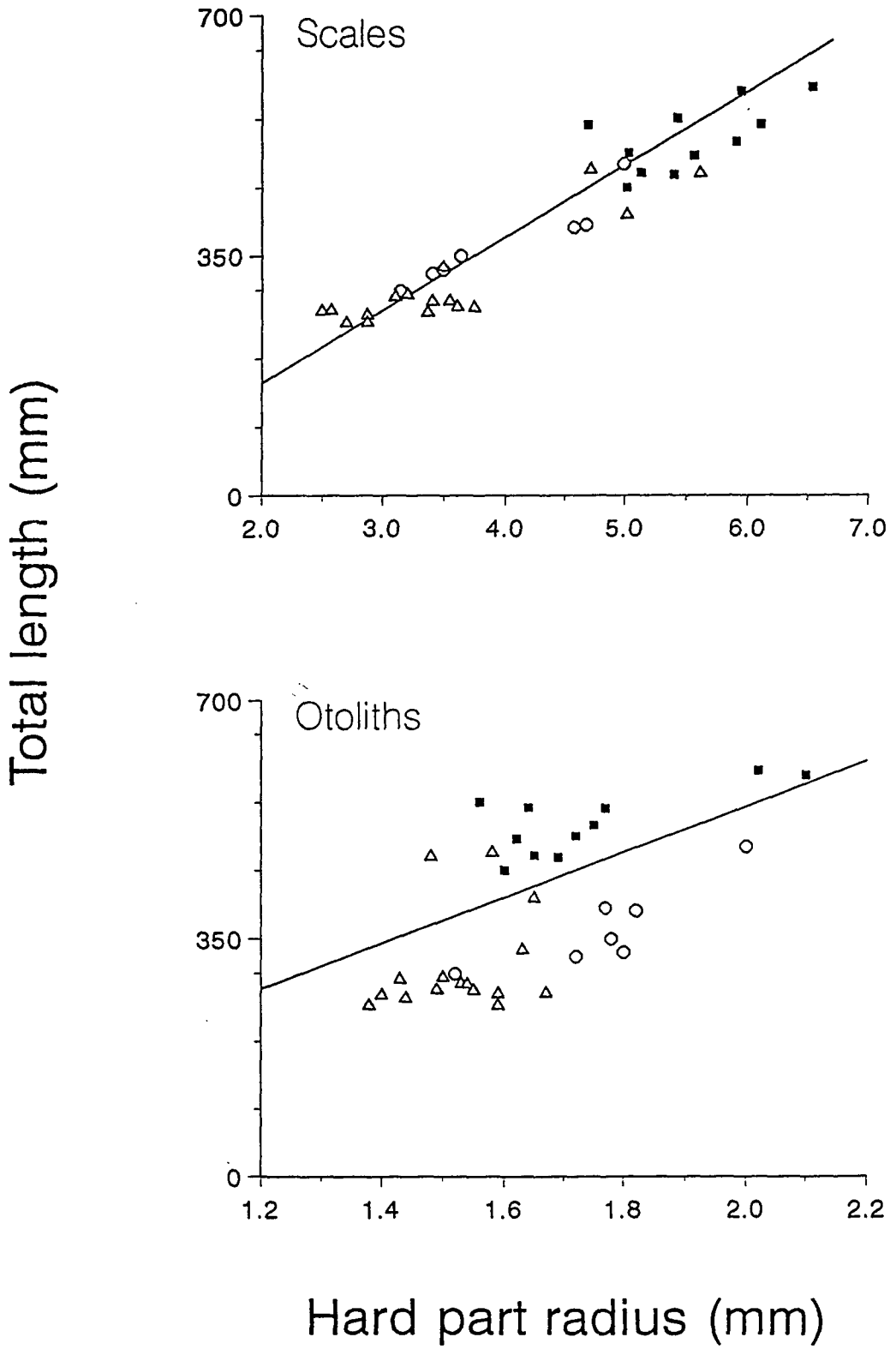

Otoliths
Scales
Relative marginal increment (%)
Month
25
20
15
10
5
0
Apr
May
Jun
Jul
Aug
Sep
Oct
27
59
27
25
20
12
3

Fig. 10. Total length plotted on hardpart size for age 3 weakfish, N=35. Lines represent the linear total length to hardpart regressions calculated from all fish, N=175. Fish are marked by season of collection: open circles=April/May; shaded triangles=June/July; and black squares= August/September.


Scales
700
350
0
2.0
3.0
4.0
5.0
6.0
7.0
Otoliths
700
350
0
1.2
1.4
1.6
1.8
2.0
2.2
Total length (mm)
Hard part radius (mm)

(Fig. 11). Equations were:

Scales:

$TL = -151.6 + 160.2\ SR - 5.4\ SR^2$ (R^2=0.96, N=88, P=0.0001)

Otoliths:

$TL = -220.9 + 543.1\ OR - 66.9\ OR^2$ (R^2=0.94, N=88, P=0.0001).

The pattern of mean annual growth increments differed between scales and otoliths. Both scales and otoliths showed their largest growth increment from the focus to the first annulus (Fig. 12). However, once fish had reached age one, the largest otolith annual growth increment occurred between the first and second annuli, whereas scales had a very small increment between these annuli. The largest scale growth increment after age one was between annuli 3 and 4. Neither hardpart showed a consistently decreasing mean annual growth increment as age increased. Although this assumption is often included in scale reading criteria, it would be inappropriate for weakfish.

Back-calculated mean body sizes-at-age were larger for scales than for otoliths (Table 3). In part, this discrepancy may reflect different times of annulus formation: back-calculated lengths from scales, in general, estimate sizes in August, whereas back-calculated lengths from otoliths estimate sizes in April and May. In addition,

Fig. 11. Weakfish total length on hardpart radius regression used for back-calculation. Based on fish collected in April and May, N=88.

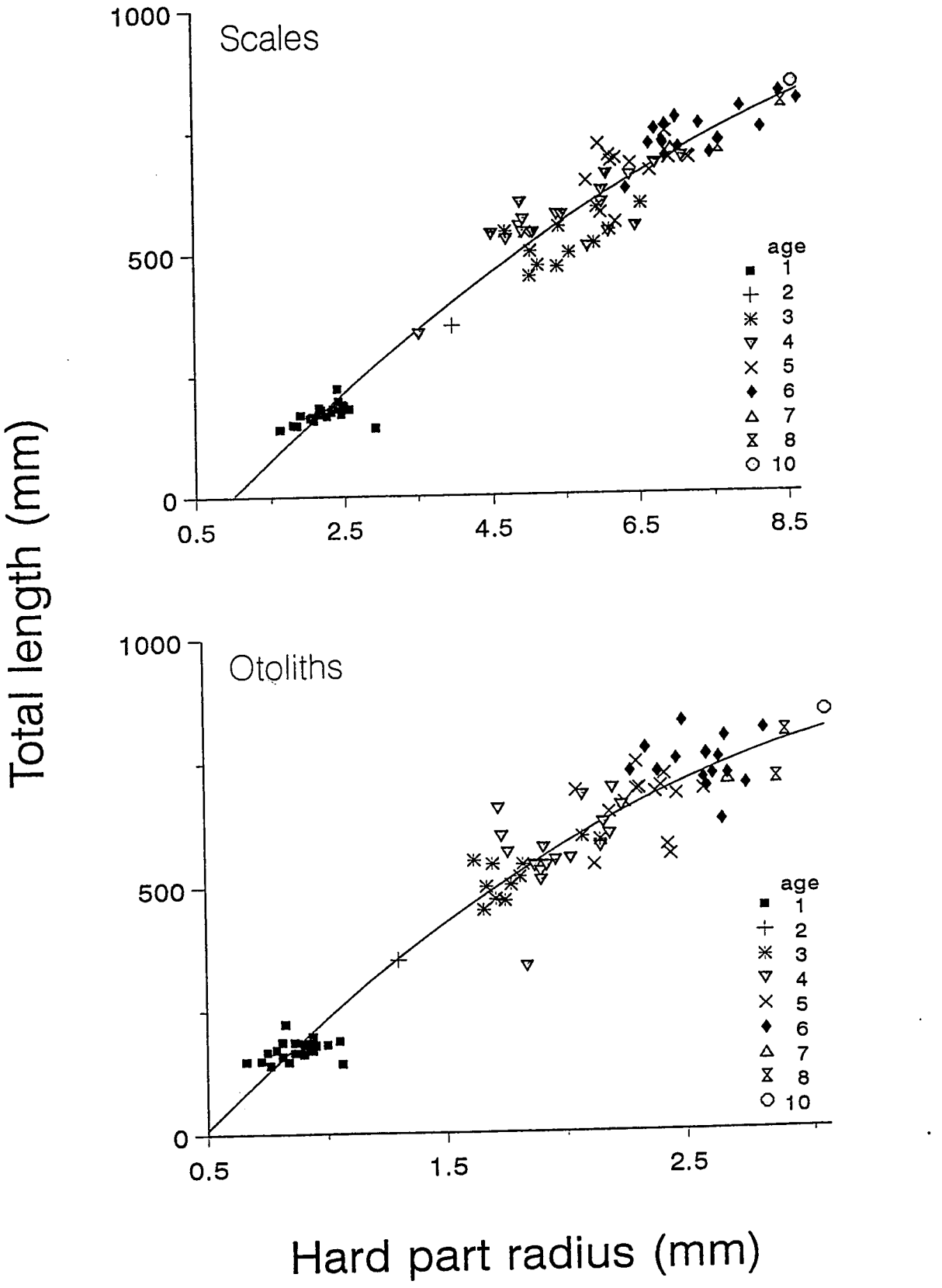

Scales
1000
500
0
0.5
2.5
4.5
6.5
8.5
age
1
2
3
4
5
6
7
8
10
Otoliths
1000
500
0
0.5
1.5
2.5
age
1
2
3
4
5
6
7
8
10
Total length (mm)
Hard part radius (mm)

Fig. 12. Mean annual growth increments of weakfish scales and otoliths. Vertical bars are ± one standard error. Numbers above the bars represent sample sizes.

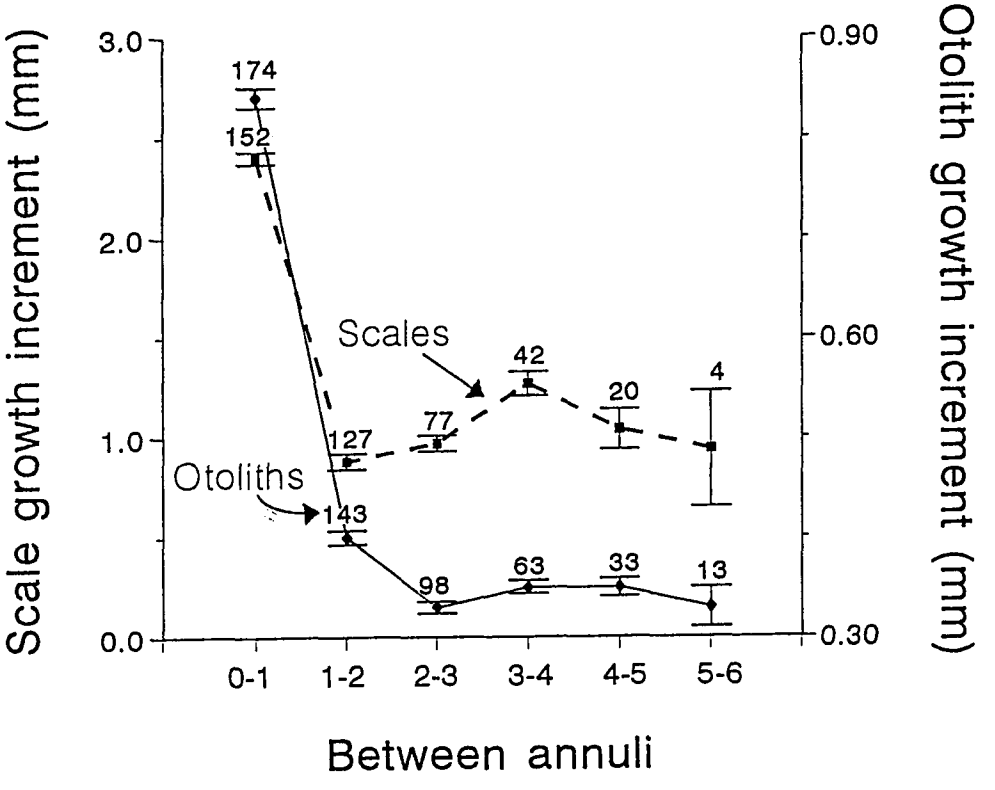

Scale growth increment (mm)
Otolith growth increment (mm)
3.0
2.0
1.0
0.0
0.90
0.60
0.30
174
152
127
143
77
98
42
63
20
33
4
13
Scales
Otoliths
0-1
1-2
2-3
3-4
4-5
5-6
Between annuli

Table 3. Mean back-calculated weakfish total lengths (mm) at age based on scales and otoliths, calculated from a quadratic body to hardpart regression and observed mean total length at time of annulus formation. Sample size is in parentheses.

Age	Scales	Observed Jul/Aug	Otoliths	Observed April/May
1	196 (152)	240 (7)	162 (174)	172 (22)
2	305 (127)	296 (25)	297 (144)	260 (2)
3	422 (77)	377 (8)	421 (99)	532 (12)
4	564 (42)	514 (5)	552 (64)	566 (18)
5	682 (20)		660 (34)	663 (14)
6	733 (4)		711 (14)	741 (16)
7			750 (5)	710 (1)
8			748 (2)	759 (2)
10				845 (1)

at older ages, back-calculated body sizes-at-age based on scales would be expected to be larger due to the underageing of older fish by scales.

Both scales and otoliths showed smaller back-calculated mean body size-at-age 1 than observed. At later ages, back-calculated TLs from scales were larger than observed, while back-calculated TLs from otoliths showed no consistent trend (Table 3). The cause of the smaller back-calculated TLs at age 1, however, did not appear related to Lee's phenomenon, as there was no consistent trend of smaller age 1 annular radii at older ages at capture (Tables 4 & 5). In fact, the largest mean SAR and OAR at age 1 came from 5-year-old fish. However, age 1 OARs from the oldest fish in the study (> age 6, N=5) were distinctly smaller than those observed in younger fish.

Table 4. Mean scale annular radii (SAR), for each scale age of weakfish.

		Scale annulus					
Age	N	1	2	3	4	5	6
1	12	2.59					
2	52	2.31	3.20				
3	24	2.40	3.42	4.14			
4	29	2.38	3.27	4.27	5.56		
5	16	2.65	3.44	4.31	5.43	7.15	
6	16	2.38	3.25	4.30	5.58	6.64	7.00
7	3	2.11	3.09	3.92	5.65	6.69	7.37

Table 5. Mean otolith annular radii (OAR), for each otolith age of weakfish.

		Otolith annulus							
Age	N	1	2	3	4	5	6	7	8
1	29	0.83							
2	45	0.85	1.27						
3	35	0.82	1.21	1.56					
4	30	0.82	1.20	1.53	1.91				
5	14	0.88	1.25	1.58	1.91	2.28			
6	16	0.86	1.22	1.54	1.88	2.21	2.52		
7	2	0.80	1.18	1.47	1.79	2.16	2.47	2.79	
8	2	0.77	1.20	1.56	1.90	2.22	2.47	2.65	2.85
10	1	0.67	1.11	1.52	1.94	2.15	2.32	2.49	2.67

DISCUSSION

My results indicate that transverse otolith sections are the best method to age weakfish. Sectioned otoliths were characterized by thin opaque bands, considered annuli, interspersed with wider translucent zones. This pattern is similar to other sciaenids, such as: spotted seatrout, Cynoscion nebulosus (Maceina et al. 1987), Atlantic croaker, Micropogonias undulatus (Barbieri et al. 1994), red drum, Sciaenops ocellatus (Murphy & Taylor 1991), and black drum, Pogonias cromis (Beckman et al. 1990) and should not be confused with the more common otolith pattern found in many temperate fish of thin translucent zones, which are considered annuli, interspersed with wide opaque zones (Hyndes et al. 1992).

Sectioned otoliths were consistently clear and easy to read, as shown by the high precision of repeated age readings. Although it was possible only to validate ages 1-5 by separate marginal increment plots, otolith annuli in all ages examined (1-10) were laid down once a year during a discrete time period (April-May). The constancy of annulus deposition at older ages, the lack of severely crowded

annuli in older fish, and the similarity between weakfish otoliths and other sciaenid otoliths which have been validated at older ages (Beckman et al. 1990, Murphy & Taylor 1991, Barbieri et al. 1994) highly suggest that otoliths are a reliable ageing technique for weakfish, although older ages must still be validated.

In contrast, I found the scale method of ageing weakfish to be imprecise and apparently inaccurate at older ages. I found scales form annuli over an extended period, April-August, similar to the results of past studies (Perlmutter et al. 1956, Massmann 1963b). This protracted period of annulus formation made it difficult to assign ages to fish taken in mid-summer with moderate growth on the scale margin, as Massmann (1963b) noted. For example, a fish taken in July with a medium marginal increment on its scale could have formed its annuli in early April and have grown since then, or it could be increasing its growth increment before forming an annulus in August. Thus, assigning an age to these fish is purely subjective and can lead to ageing errors +/- one year, which may explain most of the discrepancies between otolith and scale ages.

The long period of annulus formation on scales and severe crowding of annuli at older ages make it difficult to validate scales by the marginal increment method—as Perlmutter et al. (1956) and Shepherd & Grimes (1983) attempted for pooled age data. Because scale annuli form

over a protracted period, the trough in the marginal increment plot is shallow and the range of marginal growth during other months is large. Additionally, validation by the marginal increment method is not appropriate if the hardpart shows severe crowding of annuli at older ages, as I found with scales, and has been previously reported (Shepherd 1988). Shepherd (1988) described annuli in fish older than age 6 or 7 as being crowded and very difficult to detect, which could lead to marginal increments being measured from the last distinguishable annulus to the edge, rather than from the last real annulus to the edge. This error would inflate marginal increment estimates and there would be no way to detect underaged, older fish in marginal increment plots.

The scale method appears to underage older weakfish. Assuming otolith ages were valid, 4 of the 5 fish in this study older than age 6 were underaged by scales. Although 4 out of 155 fish may seem insignificant, the importance of correctly ageing these fish cannot be judged only by the number of discrepancies. These fish represent the beginning of an asymptote in growth and fish in the asymptotic range are often rare in highly-exploited stocks. Obtaining and correctly ageing a few weakfish in this range is critical to correctly estimating the parameters of the von Bertalanffy growth curve.

Annulus formation on weakfish otoliths and scales shows

different patterns. The formation of otolith annuli over a discrete time period suggests it may be caused by environmental variables. The most commonly suggested environmental influences on annulus formation are: temperature, salinity, food and light (Simkiss 1974). Weakfish form annuli on their otoliths in April and May, which corresponds to when they migrate from offshore winter grounds to estuarine feeding and spawning grounds. Thus, annulus formation may be linked to their movement into a different environment.

Weakfish scales, in contrast, have a more variable time of annulus formation, suggesting a cause other than general environmental conditions. Scales may undergo resorption, whereas otoliths do not (Simkiss 1974) and spawning has been linked to scale resorption with a consequent scale mark in salmon and trout (Crichton 1935). Spawning may also be linked to formation of annuli on weakfish scales (Merriner 1973). Weakfish mature at age 1 (Merriner 1976, Shepherd and Grimes 1984), and are multiple spawners with a protracted spawning period from May through August (see Chapter 3). However, individual spawning periods are asynchronous and vary greatly, especially in time of termination. Spawning activity and annulus formation may be linked in two ways: (1) annuli could form on scales early in the spawning season, when resources are shifted towards production of reproductive materials—especially the yolking

of oocytes; or (2) annuli might form near the end of the season, due to the cumulative drain of protracted spawning, causing a cessation in growth and thus an annulus. A connection between scale annulus formation and spawning in weakfish would explain the high level of variation in when annuli form, as well as the higher accuracy of ages based on scales taken from females—as females usually invest more energy in reproduction. It might also explain the small growth increment between annuli 1 and 2, if 1-year-old weakfish begin spawning later in the season than older fish, due to a threshold size necessary to reach maturity (Merriner 1973, see Chapter 3).

My results indicate both scales and otoliths present problems for back-calculation of weakfish. Although scales showed a strong relationship between body and hardpart size and no seasonal differences in growth, their long and variable time of annulus formation may cause considerable error (Smith 1983). It is impossible to determine if a fish formed its annuli at the same time each year. Because annuli can form from April-August, increments may represent 8-16 months of growth, rather than remaining constant at approximately one year. Additionally, scale annuli are more difficult to distinguish than otolith annuli, making SARs difficult to measure and somewhat subjective. However, otoliths showed seasonal change in the body to hardpart relationship, making a season specific back-calculation

equation, such as I developed, inappropriate for fish collected outside of that season. Additionally, comparisons between back-calculated and observed sizes at age were complicated by the weakfish migrational pattern, since weakfish age ranges in the Chesapeake Bay vary seasonally—older fish occurring only in spring and occasionally, fall (Joseph 1972).

There was no clear evidence of Lee's phenomenon, as older fish did not consistently show smaller hardpart size at younger ages. The five oldest fish did, however, demonstrate considerably smaller OARs at age 1 than their younger counterparts. Nevertheless, these same fish did not demonstrate consistently smaller OARs at consecutive ages than younger fish. Thus, the smaller OARs at age 1 may simply reflect when most fish of those year-classes were born, i.e., fish born early in the spawning season would have larger OARs at age 1 because they had more time to grow before winter, than fish born later in the season.

Previous criticism of back-calculation has focused mainly on the body size to hardpart relationship and its calculation (Casselman 1990, Campana 1990, Francis 1990, Ricker 1992). However, the validity of back-calculation also depends on the constancy, clarity and pattern of hardpart growth increments. The different growth increment patterns I found between scales and otoliths demonstrates the need to better understand hardpart growth, how it

relates to somatic growth and what causes annulus formation on different hardparts.

Future studies of weakfish age and growth should be based on sectioned otoliths as scales appear inaccurate once growth becomes asymptotic. This common failing of the scale method has been reported for many species (Beamish & McFarlane 1987). It can result in underestimates of longevity, overestimates of mortality, inaccurate growth calculations and improper modelling and management decisions (Beamish & McFarlane 1983). Similarly, current estimates of weakfish growth, longevity and mortality may need to be reevaluated, as suggested by my findings that scales underage older fish and have crowded annuli past age 6. The need for this reevaluation is underscored by the occurrence of a 17-year-old, as aged by otoliths, which was previously aged as a 7-year-old by scales (see Chapter 2).

CHAPTER 2

Age and growth

INTRODUCTION

Although weakfish have been important in Atlantic coast fisheries since the 1800's (Mercer 1985), weakfish landings have widely fluctuated (General Introduction). Concurrent with fluctuations in presumed abundance, have been changes in maximum size and age (Massmann 1963a, Joseph 1972, Feldheim 1975, Villoso 1989). For example, in Chesapeake Bay, the largest reported weakfish was 16 lbs (7.3 Kg) in 1921 (Hildebrand and Schroeder 1928). However, by the mid-1950's, when landings were low, Massmann (1963a) found average size had decreased and few fish weighed more than 2 lbs (0.91 Kg). Large fish again became common in Chesapeake Bay as the fishery recovered in the 1970's and early 1980's—a 19-lb (8.6 Kg) weakfish being caught in Chesapeake Bay in 1983.

To understand what causes fluctuations in weakfish landings and abundance, it is necessary to understand age structure and growth, and how they vary regionally and temporally. Although there have been many studies on weakfish age and growth (e.g., Taylor 1916, Nesbit 1954, Perlmutter et al. 1956, Massmann 1963a, Merriner 1973,

Feldheim 1975, Seagraves 1981, Shepherd and Grimes 1983, Hawkins 1988), all have been based on scales—an inappropriate method because scales underage older fish of many species (Beamish and McFarlane 1987) including weakfish (see Chapter 1). Thus, ages based on scales can lead to inappropriate growth and mortality estimates, which can affect yield modelling results and management decisions.

Weakfish age and growth have been reported to vary geographically, increasing with latitude (Pearson 1932, Nesbit 1954, Shepherd and Grimes 1983). However, it is unclear whether these differences are due to different population segments (Nesbit 1954, Perlmutter et al. 1956, Seguin 1960) or to differential migration (Vaughan et al. 1991). Regardless of the cause, if these differences exist, estimates of growth and longevity throughout the weakfish range will be necessary for proper management. However, weakfish age and growth in the Chesapeake Bay region has not been studied since Massmann (1963a). A current study is necessary because: (1) Massmann (1963a) based his ages on scales; and (2) changes in landings and maximum size and age suggest weakfish age structure may have changed since Massmann (1963a).

This study was undertaken to determine the current age structure and growth of weakfish in the Chesapeake Bay region, using a validated ageing method (Chapter 1). The hypothesis that weakfish in the Chesapeake Bay region obtain

a lower maximum size and age than in Delaware Bay (Shepherd and Grimes 1983) is evaluated, and historic trends in maximum size and numbers of large fish in Chesapeake and Delaware Bays are evaluated.

MATERIAL AND METHODS

A total of 3,630 weakfish were collected in 1989-1992 from pound net, haul seine, and gill net fisheries in the Chesapeake Bay region. On each sampling date either a 22.7 Kg (50 lb) box of each available market grade (small, medium, or large) or the total catch was purchased and processed for biological data (see below). Boxes could not be randomly selected, but Chittenden (1989) found little or no variation in size among boxes, within grades. To obtain year-round samples, 344 fish were collected in winter (when weakfish do not occur in Chesapeake Bay) from the trawl fishery operating in Virginia and North Carolina shelf waters north of Cape Hatteras. To ensure enough age 1 fish for growth estimates, an additional 200 age 1 and young-of-the-year fish were collected by the VIMS juvenile trawl survey, since age 1 fish are not fully-recruited to commercial foodfish grades (See Size/Age Compositions and Mortality section in Results). Details on sampling design and gear of the VIMS survey can be found in Chittenden (1989a) and Geer et al. (1990).

To increase the number of older fish in this study, so

that maximum sizes and ages in Chesapeake Bay and Delaware Bay could be compared, and the asymptotic size range could be better defined: (1) 34 fish were collected from the 1992 World Championship Weakfish Tournament in Dover, DE; (2) in 1992/1993, 10 fish from Delaware Bay ≥ 3.6 Kg total weight, and 5 fish from Chesapeake Bay ≥ 3.6 Kg total weight were selected from commercial catches and processed for biological data; and (3) otoliths, sex and size of 44 fish ≥ 500 mm total length collected in Delaware Bay in 1985/1986 by Villoso (1989) were analyzed. To evaluate historic trends in maximum size and numbers of large fish, the annual number of citation size fish and the total weight of the largest fish reported were obtained from the Virginia Saltwater Fishing Tournament (1958-1992) and from the Delaware State Fishing Tournament (1968-1992).

In general, collections were processed for biological data as follows: fish were sexed and measured for total length (TL) to the nearest millimeter, and weighed for total gutted weight (TGW) and gonad weight (GW) to the nearest gram. Gutted weights were used because weakfish are piscivorous and can swallow fish a third of their own weight, which would greatly bias somatic weights. Somatic weight (SW) was calculated as TGW-GW. Standard length (SL) and girth (G) were also measured to the nearest millimeter for 672 fish.

Otoliths from 3,298 fish were sectioned and aged using

the validated method described in Chapter 1. Because of the small sample size used in Chapter 1 (N=175), precision of age readings was again evaluated in this Chapter by percent agreement between two readers (N=1,191). More than 95% of the fish sampled were aged each year except 1990. In 1990, when many small fish were sampled, those to be aged (794 out of 2,098) were selected by systematic, random subsampling. Ages were assigned assuming January 1 as an arbitrary average birthdate (Jearld 1983, Shepherd 1988). This birthdate was selected, so that fish of the same year-class collected in April and May—before annuli form (Chapter 1)—would be assigned the same age as those collected after annuli had formed.

A probable range of instantaneous rates of total mortality (Z) were calculated based on: (1) the maximum age observed in either Chesapeake Bay or Delaware Bay; and (2) the maximum age consistently occurring in Chesapeake Bay commercial catches from 1989-1992. Rates of Z were calculated using the following equation, based on the reasoning of Royce (1972):

$$S = e^{-Ztmax}$$

where:

S = survival rate, assumed to be 0.01 at maximum age

Z = instantaneous total mortality rate

t_{max} = maximum age.

To determine if the population growth rate was representative of the true growth rate, i.e., there was not size-selective mortality within year-classes, sectioned otolith sizes-at-first-annulus were evaluated for fish ages 1-12 (Ricker 1975). Otolith radius to the first annulus was measured, as described in Chapter 1, for 403 Chesapeake Bay fish collected in 1989 and 1992/1993 and 47 Delaware Bay fish from 1992/1993. Given the strong relationship between otolith radius and TL (Chapter 1), size of the otolith at the first annulus was considered an indicator of fish size at age 1. A one-way ANOVA was used to determine if otolith sizes-at-first-annulus were significantly different by age.

Growth was evaluated using nonlinear regression (Marquardt method) to fit the von Bertalanffy model (Ricker 1975) to observed, individual lengths of Chesapeake Bay fish ages 1-12. To increase the number of fish in the asymptotic size range, three fish age 8 or older, collected from Delaware Bay in 1992/1993, were also included. To remove seasonal effects, only fish collected in April and May were used for calculations. These months were used because they are when: (1) the somatic growth season begins; (2) otolith annuli form; and (3) the largest range of sizes and ages occur in Chesapeake Bay. Finally, to test differences in

growth by sex, observed mean-sizes-at-age in Chesapeake Bay were calculated for each sex and tested using a t-test.

Linear regression was used to determine SW-TL, SL-TL and G-TL relationships for fish collected in Chesapeake Bay. SL-TL and G-TL relationships were based on pound net collections of fish ranging from 200-845 mm TL. The SW-TL relationship was based on log-transformed data from fish ranging from 188-875 mm TL and 71-6,137 g SW, collected by pound net, haul seine and gill net. Differences between sexes were tested by ANCOVA. A t-test was used to test if the slope of the SW-TL regression was significantly different from 3—a slope of 3 indicating isometric growth. When only TL was given in the literature, conversions were made using a TGW-TL relationship based on fish collected in April and May, ranging from 20-6,276 g TGW and 140-875 mm TL.

All data were analyzed using statistical methods available in SAS (1988). Model assumptions were evaluated by examination of residuals (Draper and Smith, 1981). Rejection of the null hypothesis was based on an α level of 0.05, and F-tests in ANCOVA were based on Type III sums of squares (Freund and Littell 1986).

RESULTS

Age determination

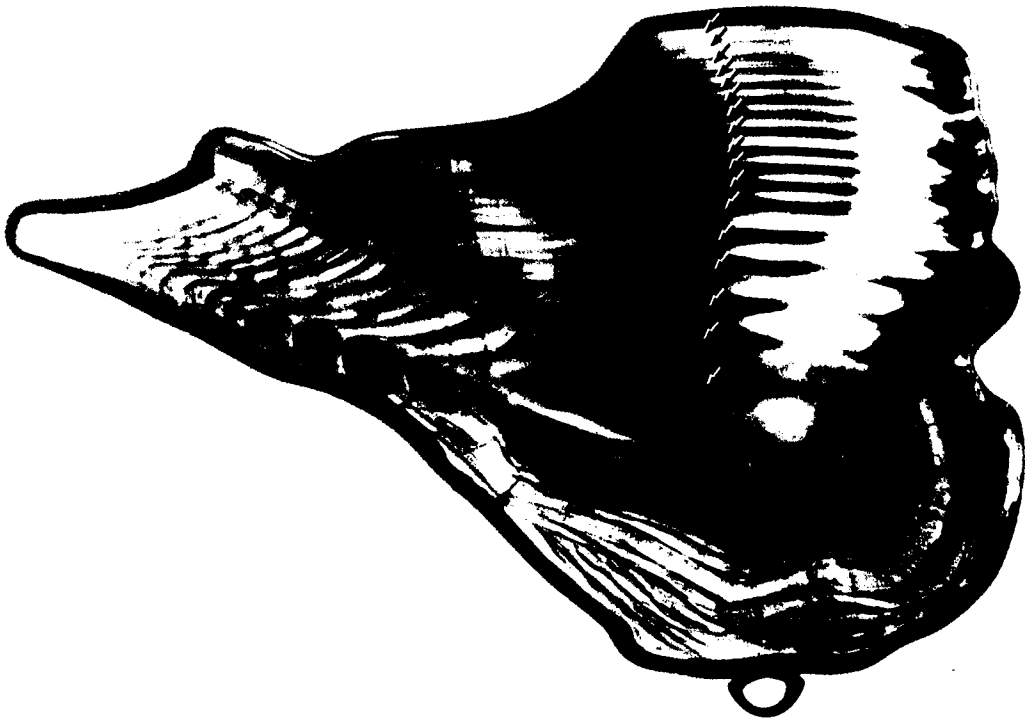
As previously described (Chapter 1), transverse sections of weakfish otoliths are extremely clear. They remained consistently so for the 3,257 fish aged in this study. Of 1,191 otoliths read by two separate readers, 99.8% of the assigned ages agreed. In addition, otolith annuli did not show severe crowding at older ages and were easily distinguished even in a 17-year-old, the oldest fish aged (Fig. 13).

Size/age compositions and mortality

Most weakfish collected from commercial fisheries in Chesapeake Bay from 1989 to 1992 were 200-600 mm TL. Mean yearly TLs were: 368 mm in 1989 (N=400), 268 mm in 1990 (N=2,079), 391 mm in 1991 (N=1,146), and 364 in 1992 (N=403). Ninety percent of the fish collected in 1989-1992 were ≤ 472 mm TL, and 99% were ≤ 652 mm TL (Fig. 14). The smallest fish observed in commercial foodfish grades were similar each year, approximately 200 mm TL, while the largest fish varied from approximately 650 mm TL in 1990 to 850 mm TL in 1989 and 1992.

Although fish from Chesapeake Bay commercial foodfish

Fig. 13. Transverse otolith section of an age 17 weakfish caught in May 1985 in Delaware Bay. Arrows indicate annuli.



grades from 1989-1992 ranged from 1 to 10 years old, most were ages 1-4 (Fig. 14). Usually age 2 fish made up most of the catch (37-51%), and 2- and 3-year-olds comprised more than half the catch (43-78%). Mean yearly ages were: 2.7 in 1989 (N=378), 1.6 in 1990 (N=775), 2.7 in 1991 (N=1,110), and 2.6 in 1992 (N=391). Fish older than age 4 were uncommon, never being more than 6% of the annual catch. Of the fish collected in 1989-1992, 90% were ≤ age 4, and 99% were ≤ age 5.

Weakfish were not fully-recruited to commercial foodfish grades until age 2. Young-of-the-year and yearling fish occurred in Chesapeake Bay, making up 99% (N=200) of the fish analyzed from the VIMS juvenile trawl survey. However, young-of-the-year were not present in commercial foodfish grades, and yearlings were not fully-recruited—as demonstrated by their generally low frequency in annual age compositions (Fig. 14).

Although weakfish size and age ranges were fairly similar from 1989-1992, annual differences did occur. In 1990, a larger percentage of small (< 300 mm TL), age 1 weakfish were collected and no fish were older than age 5 (Fig. 14). Most of these small fish (< 300 mm TL) were collected by haul seine and pound net (Fig. 15), whereas gill nets caught fish primarily in the 300-400 mm TL range.

Older, larger weakfish occurred in Chesapeake Bay primarily in the spring, when they appeared to arrive before

Fig. 14. Age and length frequencies of Chesapeake Bay weakfish by year, 1989-1992, pooled over gears. Sample sizes are indicated above each age. Total annual sample size is noted for lengths.

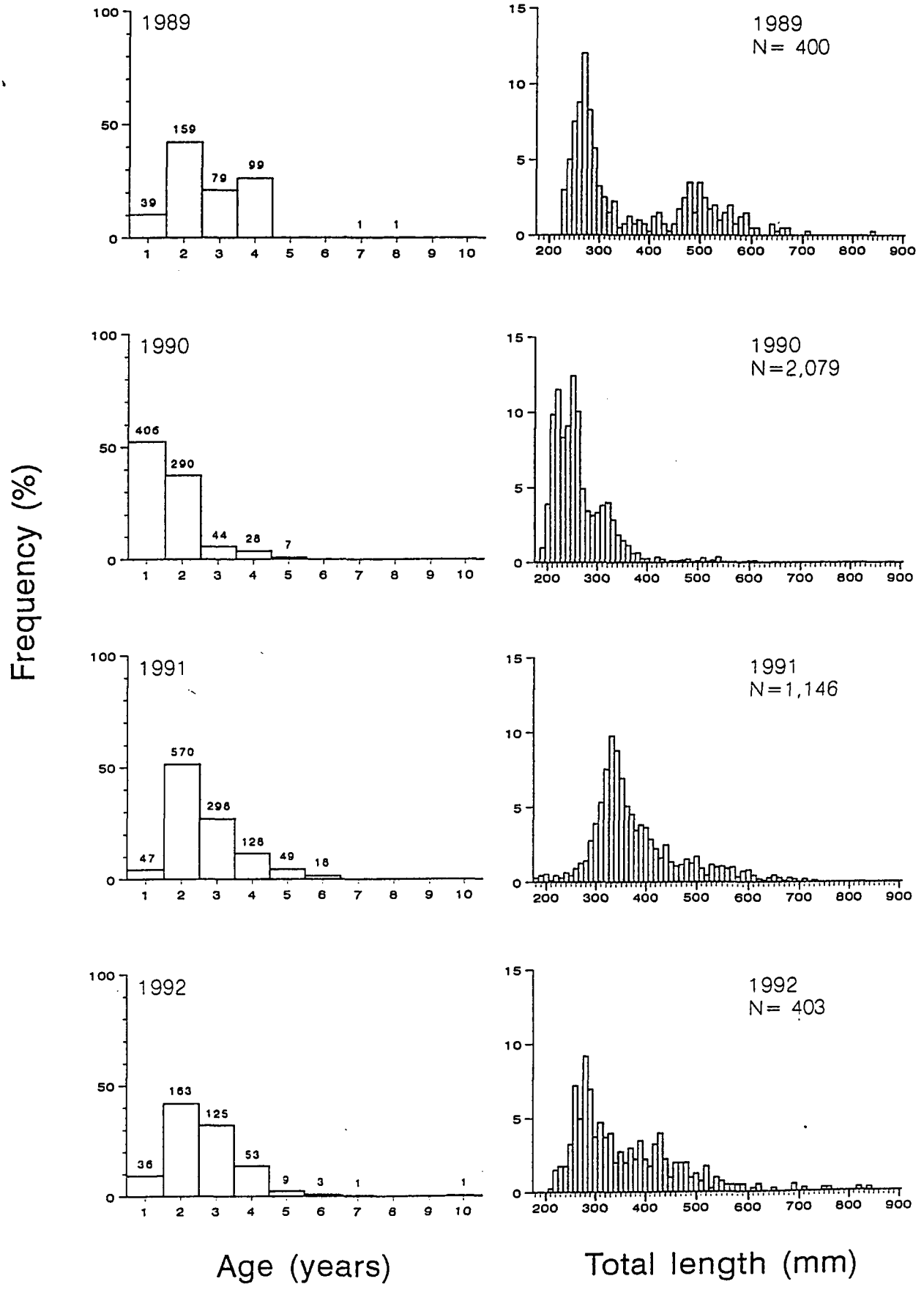
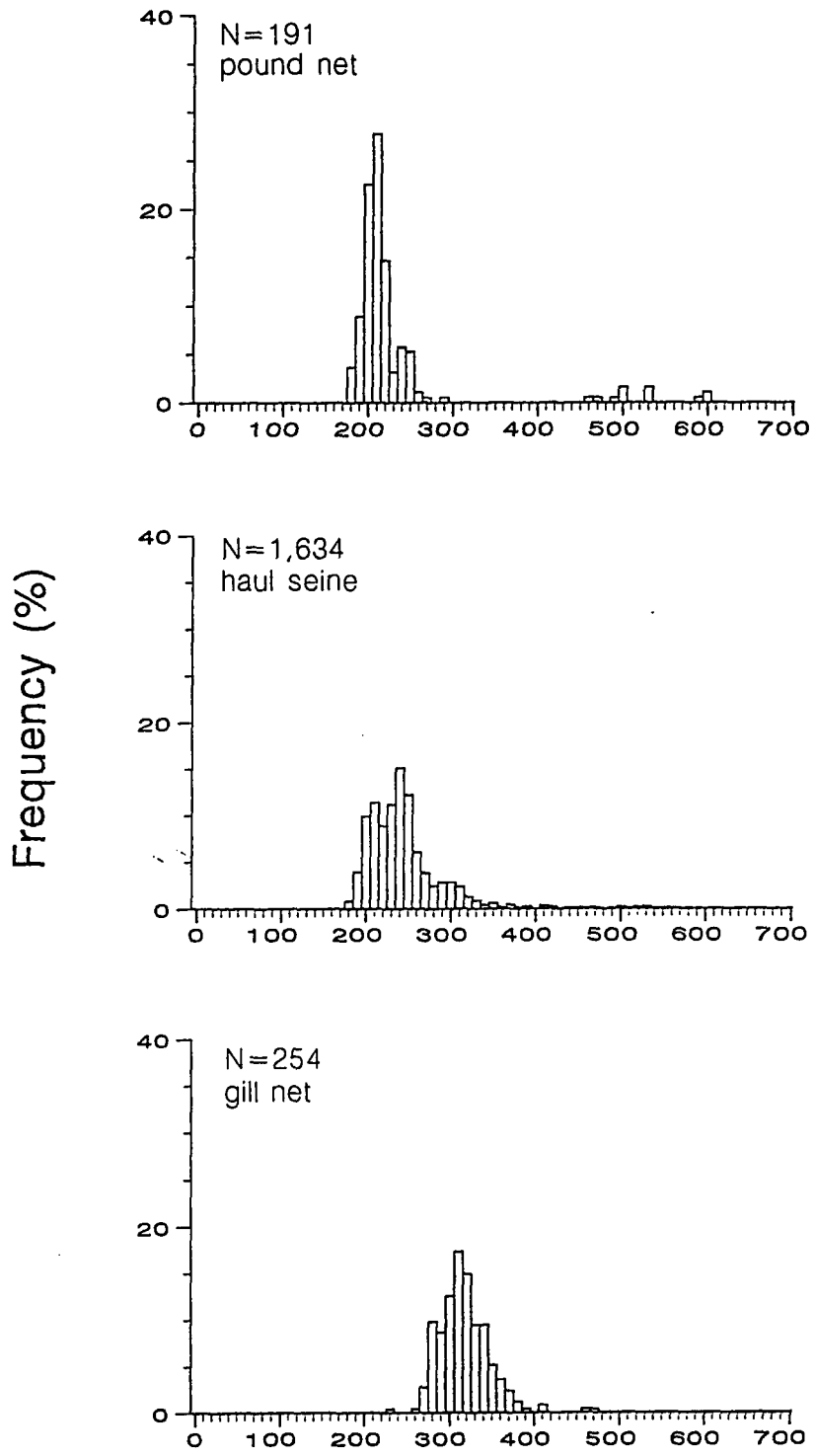

1989
39
159
79
99
1
1
1989
N= 400
1990
406
290
44
28
7
1990
N=2,079
1991
47
570
296
128
49
18
1991
N=1,146
1992
36
163
125
53
9
3
1
1
1992
N= 403
Frequency (%)
Age (years)
Total length (mm)

Fig. 15. Length frequencies of Chesapeake Bay weakfish by gear in 1990.


N=191
pound net
N=1,634
haul seine
N=254
gill net
40
20
0
0 100 200 300 400 500 600 700
Frequency (%)
Total length (mm)

younger fish. Fish age 4 and older occurred in the spring in relatively large numbers, making up 51% and 27%, of April and May catches (1989-1992), respectively (Fig. 16). However, few fish older than age 4 were caught after May, and they never made up more than 8% of the catch in later months. In contrast, few age 1 fish were observed until June, after which they made up roughly 30% of the catch.

Mean monthly size-at-age also appeared affected by migration. Mean size at ages 3-6 of Chesapeake Bay fish collected in April and May, 1989-1992, were larger than those collected in August and September (Table 6). In 1992, mean monthly TLs of age 2 and 3 fish (the most abundant ages in the catches) steadily decreased from April through July (Fig. 17). Although the pattern was less clearly defined in other years, a decrease in mean TL for age 3 fish from April to June consistently occurred and the mean TL of age 2 fish also declined from April to May in 1991 and 1992.

Maximum observed age of Chesapeake Bay weakfish was age 12. However, when fish selected for their large size were excluded, the maximum observed age was 8. Annual observed maximum age varied. Maximum observed age was 8 in 1989 (N=378), 5 in 1990 (N=775), 6 in 1991 (N=1,110), and 10 in 1992 (N=391). Of all Chesapeake Bay fish collected and aged from 1989 to 1992 (N=2,654), 99.5% were $\leq$ age 6.

Fish older than age 6 were rare in both Chesapeake Bay and Delaware Bay. Although seafood dealers in these areas

Fig. 16. Age frequency distributions of Chesapeake Bay weakfish by month, pooled over the years 1989-1992. Sample size is indicated above each bar.

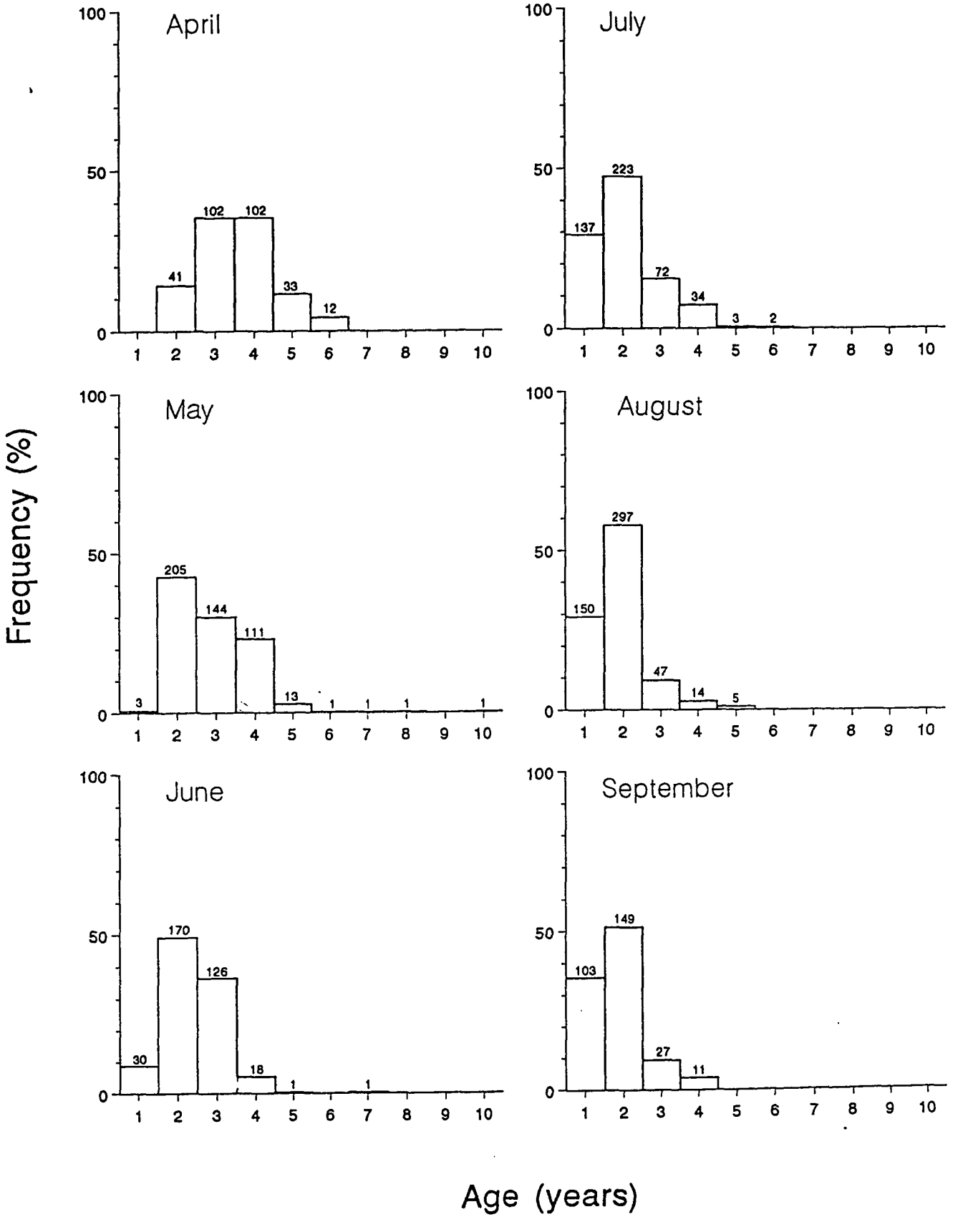
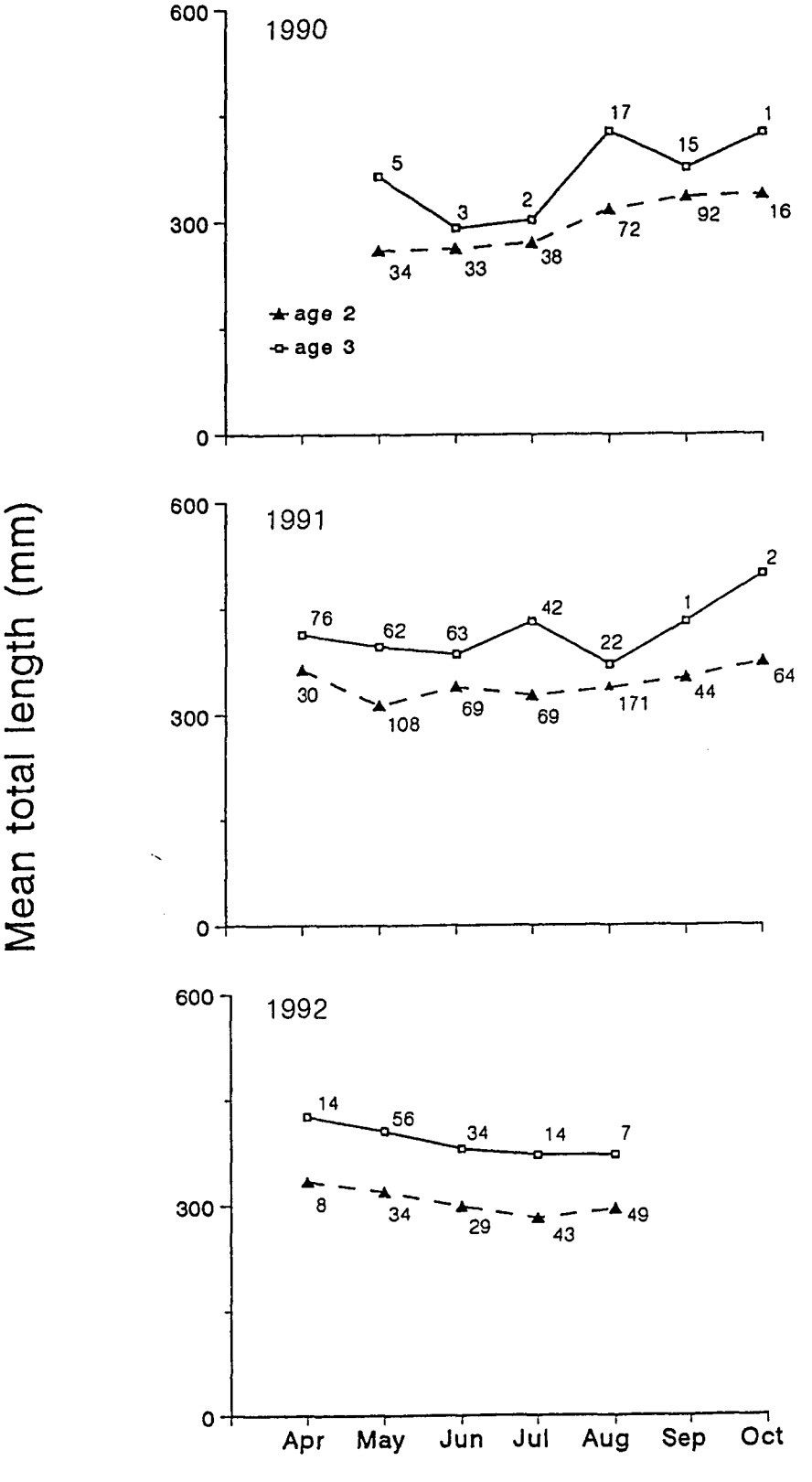

April
41
102
102
33
12
July
137
223
72
34
3
2
May
3
205
144
111
13
1
1
1
1
August
150
297
47
14
5
June
30
170
126
18
1
1
September
103
149
27
11
100
50
0
1 2 3 4 5 6 7 8 9 10
Frequency (%)
Age (years)

Table 6. Mean total length (TL) at age for Chesapeake Bay weakfish collected in April/May and August/ September, 1989-1992.

Age	N April/May	Mean (mm) April/May	N Aug/Sept	Mean Aug/Sept
1	89	176	311	251
2	246	311	516	312
3	246	411	119	402
4	213	511	50	507
5	46	558	8	549
6	13	631	2	626

Fig. 17. Mean monthly total lengths at age 2 and 3 of Chesapeake Bay weakfish, 1990-1992. Sample size is indicated next to each point.


1990
1991
1992
600
300
0
age 2
age 3
5
3
2
17
15
1
34
33
38
72
92
16
76
62
63
42
22
1
2
30
108
69
69
171
44
64
14
56
34
14
7
8
34
29
43
49
Apr
May
Jun
Jul
Aug
Sep
Oct
Mean total length (mm)
Month

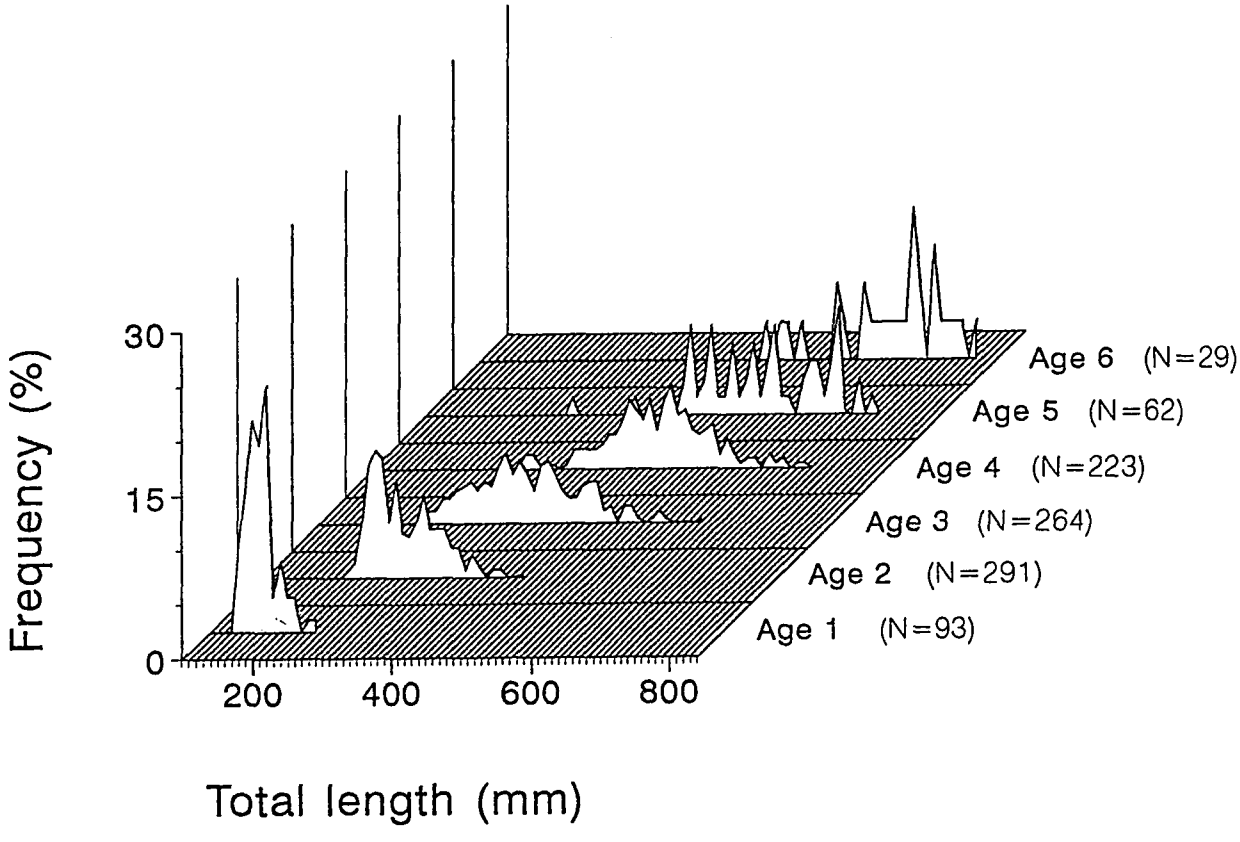
agreed to provide any fish ≥ 3.6 Kg, only four fish were collected in 1992 in Chesapeake Bay—three age 6 and one age 10. In Delaware Bay in 1992, seven fish were collected—one age 4, one age 5, four age 6, and one age 8. An additional six fish ≥ 3.6 Kg were collected at the 1992 World Championship Weakfish Tournament in Delaware, all age 6. In 1993, only four fish ≥ 3.6 Kg were collected—one age 12 fish from Chesapeake Bay, and three fish from Delaware Bay, age 6, 8 and 11.

A probable range of weakfish instantaneous mortality rates was estimated as 0.38-0.77. The lower rate was based on a maximum age of 12—the oldest weakfish observed in either Chesapeake or Delaware Bays in 1991-1992. The upper rate was calculated using a maximum age of 6—the oldest age currently found in any numbers in Chesapeake and Delaware Bays.

Growth

Weakfish size was a poor predictor of individual fish age. Except at age 1, TLs at age for fish collected in April and May showed broad ranges, much overlap, and multiple modes (Fig. 18). Because age 1 fish were not fully-recruited, their length distribution was not representative. However, the difference in size between age 1 and age 2 fish appears genuine, as only the largest age 1 fish would be selected for commercial foodfish grades. Ages

Fig. 18. Length frequencies at age for weakfish collected in April and May, pooled over gears and locations, 1989-1992.


Frequency (%)
30
15
0
200
400
600
800
Total length (mm)
Age 6 (N=29)
Age 5 (N=62)
Age 4 (N=223)
Age 3 (N=264)
Age 2 (N=291)
Age 1 (N=93)

2-5, in contrast, broadly overlapped—a fish 350 mm TL potentially being any of these ages. Weakfish also showed a large range of TGWs at age in April and May (Table 7)—a 350 g fish potentially being from age 2-5.

Observed sizes-at-age were used to estimate weakfish population growth, as there was no evidence of size-selective mortality. Mean size at first annulus showed no consistent pattern with increasing age (Table 8), and no significant differences were found between sizes-at-first annulus by age ($N=540$, $F=1.75$, $P=0.06$).

Weakfish growth was well-described by the von Bertalanffy model (Fig. 19). The von Bertalanffy curve was calculated for pooled sexes since weakfish show no readily observed sexual dimorphism. Although lengths at age were similar for both sexes, mean TLs at age were usually larger for females than males, and significantly so for ages 2 and 3 (Table 9). Mean observed TLs of pooled male and female Chesapeake Bay weakfish in April and May were: 176, 311, 412, 510, 558 and 631 mm for ages 1-6, respectively. Despite the high variability in sizes-at-age, observed lengths at ages 1-12 showed a good fit ($R^2=0.98$) to the von Bertalanffy model (Fig. 19). Estimated model parameters, asymptotic standard errors, and 95% confidence intervals are given in Table 10.

There was no evidence that weakfish from Delaware Bay reach a larger asymptotic length or size-at-age than those

Table 7. Mean total gutted weights (TGW), range and standard error at age for Chesapeake Bay and Delaware Bay weakfish collected in April and May, pooled over gears, 1989-1993.

Age	N	Mean (g)	Range (g)	Standard error
1	91	49	20-161	2.4
2	285	310	113-1,038	10.3
3	263	778	160-2,999	28.3
4	223	1,494	342-3,866	37.4
5	62	2,126	284-4,031	105.0
6	29	3,268	1,507-5,360	197.3
7	1	3,257	-	-
8	4	5,230	3,670-6,475	591.5
9	1	5,311	-	-
10	1	6,260	-	-
11	1	6,190	-	-
12	1	6,276	-	-

Table 8. Mean, range, and standard error of otolith sizes at first annulus (mm) for weakfish ages 1-12, from Chesapeake Bay and Delaware Bay.

Age	N	Mean	Range	Standard error
1	111	0.84	0.61-1.09	0.010
2	167	0.86	0.61-1.09	0.007
3	137	0.83	0.61-1.15	0.009
4	76	0.84	0.64-1.06	0.010
5	24	0.85	0.59-1.08	0.022
6	18	0.88	0.73-1.20	0.025
7	1	0.80	-	-
8	3	0.80	0.76-0.88	0.038
10	1	0.67	-	-
11	1	0.84	-	-
12	1	0.90	-	-

Fig. 19. Observed lengths-at-age and fitted von Bertalanffy regression line for Chesapeake Bay weakfish in April and May and 3 fish from Delaware Bay. Weakfish in the asymptotic size range collected in Delaware Bay in 1985/1986 are included as reference points but were not used in calculations.

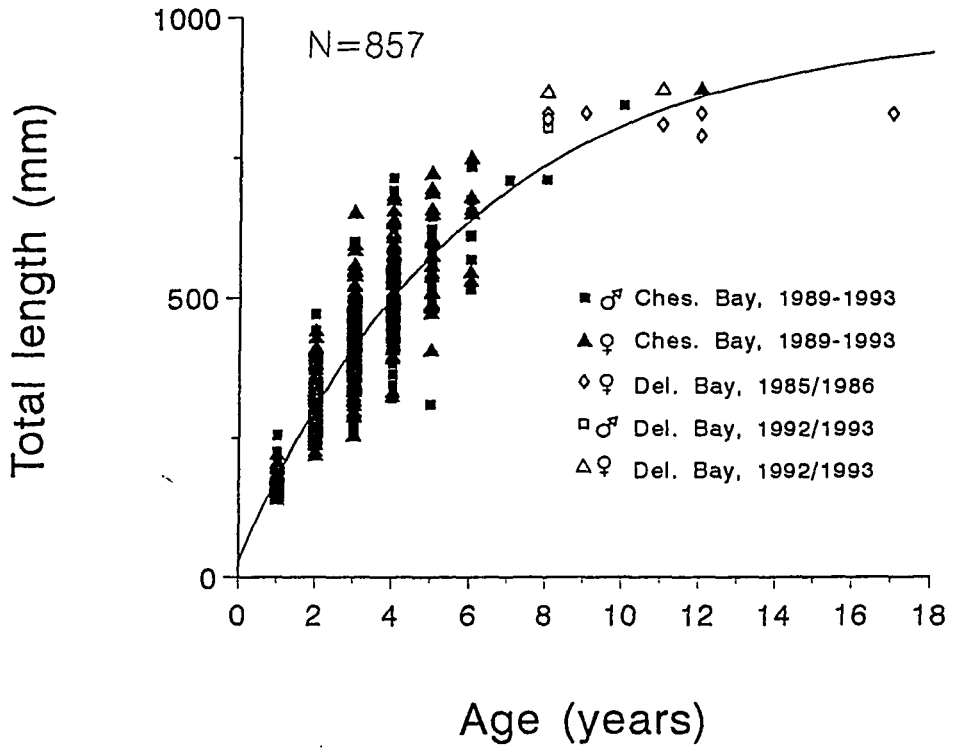

1000
500
0
N=857
Total length (mm)
0
2
4
6
8
10
12
14
16
18
Age (years)
♂ Ches. Bay, 1989-1993
♀ Ches. Bay, 1989-1993
♀ Del. Bay, 1985/1986
♂ Del. Bay, 1992/1993
♀ Del. Bay, 1992/1993

Table 9. Mean total length (mm) at age by sex of male and female weakfish from Chesapeake Bay in April and May, and t-test results. α=0.05, * P < 0.05.

Age	Mean TL males	N	Mean TL females	N	t	Significance
1	176.3	42	175.9	47	0.14	NS
2	295.8	76	318.3	170	3.33	*
3	376.5	70	425.7	174	5.10	*
4	501.8	100	518.0	112	1.67	NS
5	553.9	24	562.5	22	0.37	NS
6	735.0	7	752.0	6	0.40	NS

Table 10. Von Bertalanffy model parameter estimates, standard errors and 95% confidence intervals for weakfish in the Chesapeake Bay region.

Parameter	Estimate	Standard error	95% Confidence intervals
L_∞	983.57	60.98	863.88 - 1103.25
K	0.17	0.02	0.14 - 0.21
t_0	-0.18	0.08	-0.35 - -0.02

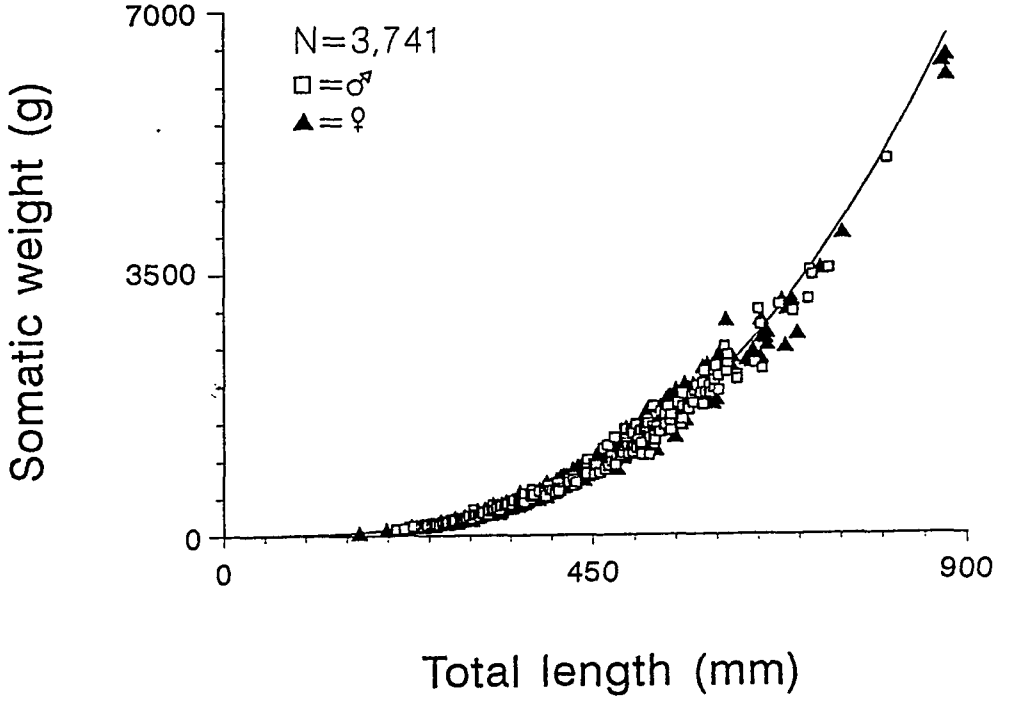
in Chesapeake Bay. Given the broad size distributions at younger ages, the 10 fish from Delaware Bay ≥ age 8 all fell within a reasonable size range when plotted against the predicted growth curve (Fig. 19). Although age 8 fish from Delaware Bay were somewhat larger than the one fish collected from Chesapeake Bay, the opposite was true for age 12 fish. In addition, of the 35 age 3-6 fish from Villoso's 1985/1986 collections, only one age 4 fish was larger than the size range observed in Chesapeake Bay. No fish (N=34) from the 1992 weakfish tournament in Dover, DE, were larger than the Chesapeake Bay size range.

Although no sexual dimorphism is apparent in weakfish, weight-length, length-length and girth-length relationships differed significantly by sex (ANCOVA, $P>0.05$). These differences were slight and probably detected only because of the large sample sizes, since equations and coefficients of determination were similar for both sexes. Thus, only equations for pooled sexes are presented. The SW to TL relationship (Fig. 20) was:

$$SW = 6.0 * 10^{-6} TL^{3.04} \quad (R^2=0.99, N=3,742)$$

The slope (b=3.04, SE=0.005) was not significantly different from 3 (t-test, t=0.002, $P<0.01$) indicating isometric growth

Fig. 20. Somatic weight-length relationship of weakfish in the Chesapeake Bay region, 1989-1992.


7000
3500
0
N=3,741
□=♂
▲=♀
0
450
900
Somatic weight (g)
Total length (mm)

The TGW to TL relationship for April and May was:

$$TGW = 4.7 * 10^{-6} TL^{3.13} \quad (R^2=0.99, N=950).$$

The G (mm) to TL (mm) relationship was:

$$G = -3.63 + 0.54 TL \quad (R^2=0.95, N=672)$$

$$TL = 23.34 + 1.76 G \quad (R^2=0.95, N=672).$$

The SL (mm) to TL (mm) relationship was:

$$SL = -11.23 + 0.88 TL \quad (R^2=0.99, N=672)$$

$$TL = 13.72 + 1.13 SL \quad (R^2=0.99, N=672).$$

Historic trends in maximum size and age

Older weakfish were collected in Delaware Bay in 1985-1986 than in 1992-1993. The average age of fish ≥ 3.6 Kg in 1985-1986 was 9.6, significantly higher than the average age of 6.4 in 1992-1993 ($t=3.14$, $DF=24$, $P<0.05$). Of the 10 fish ≥ 3.6 Kg in 1985-1986, there were: one age 4, one age 6, two age 8, two age 9, one age 11, two age 12, and one age 17. In contrast, the maximum age observed in 1992-1993 was only 11, much younger than the 17-year-old observed in 1985-1986.

Maximum sizes of weakfish began to greatly increase in Chesapeake and Delaware Bays in the early 1970's, concurrent with the recovery of the weakfish fishery. From 1958-1968,

the largest weakfish reported to the Virginia Saltwater Fishing Tournament weighed 3.1 Kg (Fig. 21). Similarly, the largest fish caught in Delaware Bay in 1968/1969 (when records began) was 2.6 Kg. However, in 1970, maximum size in Chesapeake Bay was > 3.1 Kg for the first time since 1958, and maximum size in Delaware Bay went from 2.6 Kg in 1969 to 3.9 Kg in 1970. By 1973, maximum size had more than doubled compared to what it was in the late 1960's, to 6.4 Kg in Virginia and 5.9 Kg in Delaware. Maximum sizes continued to increase until 1985, and remained high until 1989 in Virginia, and 1990 in Delaware.

The number of large fish in Chesapeake and Delaware Bays also increased in the early 1970's, concurrent with the increase in maximum size. From 1958-1968, only 64 fish > 1.8 Kg were reported in Virginia (Fig. 22). Similarly in 1968/1969, only 13 fish > 1.4 Kg were reported in Delaware Bay. However the number of fish > 1.8 Kg reported in Virginia increased from 2 in 1969 to 83 in 1970. Similarly, in Delaware Bay, the number of fish > 1.4 Kg increased from 12 in 1969 to 121 in 1970. By 1980, 1,399 fish > 5 Kg received citations in Virginia and 1,229 fish > 4.6 Kg received citations in Delaware.

Both Chesapeake and Delaware Bays have recently shown a marked decrease in maximum size and numbers of large weakfish. The number of large fish reported in Virginia dropped sharply in 1981, and has remained low since then.

Fig. 21. Maximum total weights of weakfish reported in the Delaware Sport Fishing Tournament and the Virginia Saltwater Fishing Tournament, 1958-1992. The oldest and two heaviest fish from the present study are included as reference points.

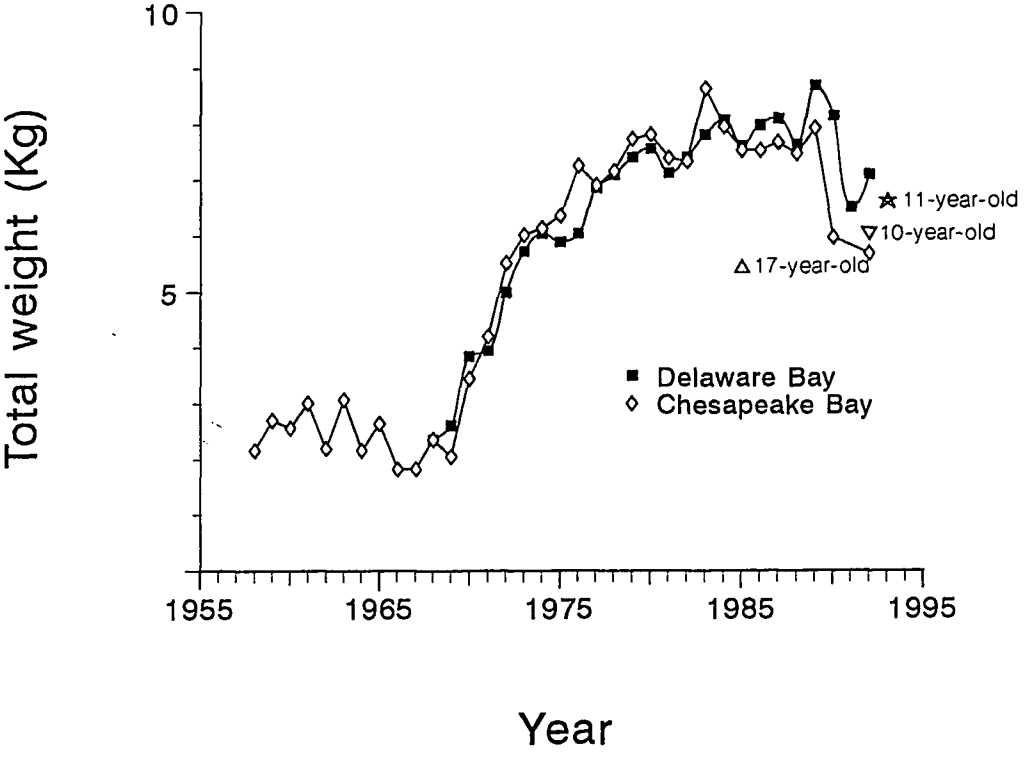
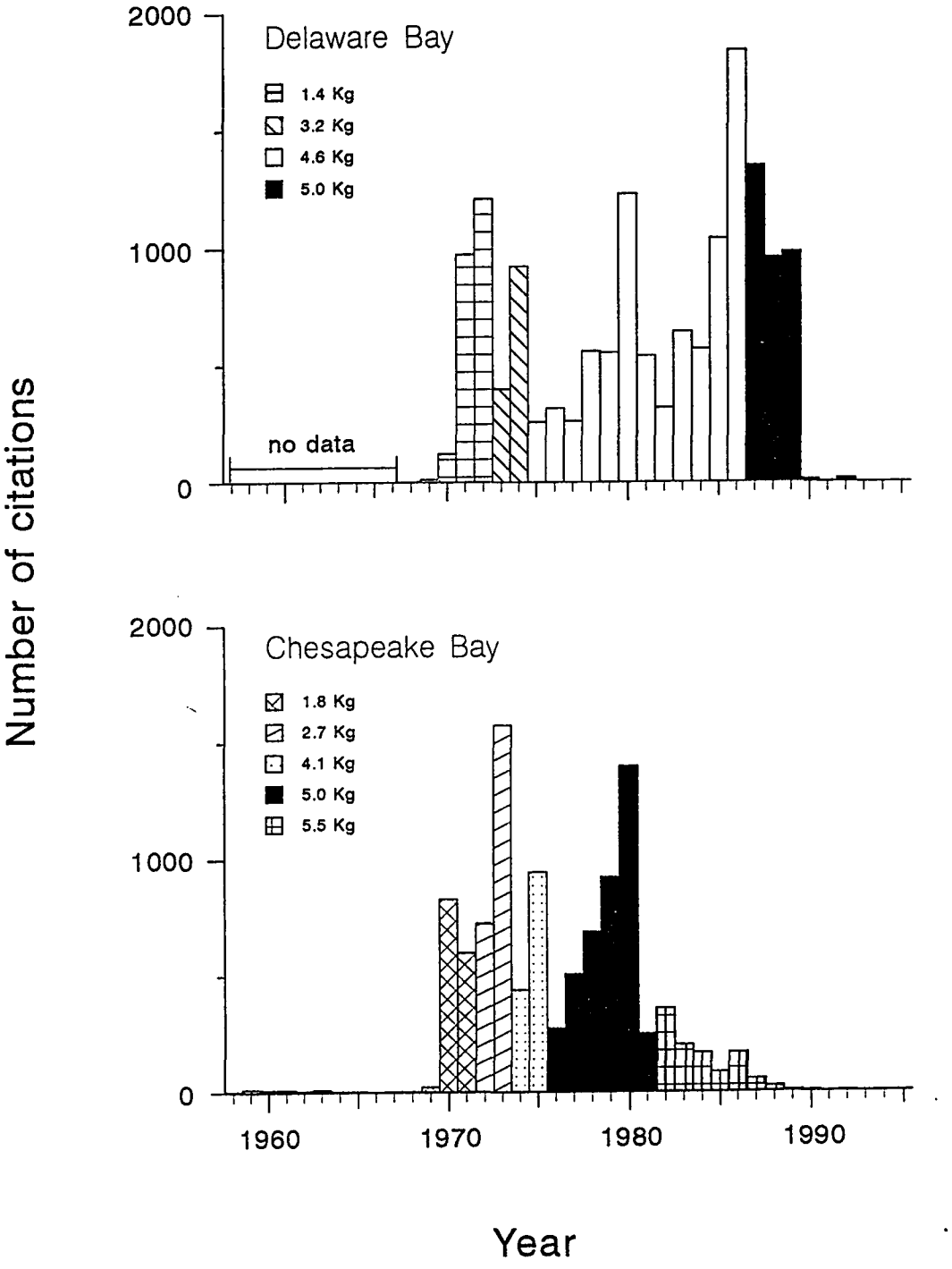

Total weight (Kg)
10
5
1955
1965
1975
1985
1995
Year
11-year-old
10-year-old
17-year-old
Delaware Bay
Chesapeake Bay

Fig. 22. Number of weakfish citations reported in the Delaware Sport Fishing Tournament and the Virginia Saltwater Fishing Tournament. Minimum citation weights are indicated by year. In 1972, the Delaware citation weight changed mid-year from 1.4 to 2.3 Kg.


Delaware Bay
1.4 Kg
3.2 Kg
4.6 Kg
5.0 Kg
no data
2000
1000
0
Chesapeake Bay
1.8 Kg
2.7 Kg
4.1 Kg
5.0 Kg
5.5 Kg
2000
1000
0
1960
1970
1980
1990
Number of citations
Year

Only 12 fish > 5.45 Kg were reported in 1989/1990, no fish in 1991, and 3 fish > 5.0 Kg in 1992. From 1990-1992, maximum size in Virginia was below 6 Kg for the first time since 1972. Delaware Bay reported large numbers of fish > 4.6 Kg until 1989. However, the number of fish > 5.0 Kg decreased from 981 in 1989 to 11 in 1990. Only 18 fish have been reported since then. In 1991, maximum size of Delaware Bay fish dropped below 7.5 Kg for the first time since 1981, and it remained low in 1992.

DISCUSSION

Size/age composition and mortality

Most weakfish in Chesapeake Bay from 1989 to 1993 were 200-600 mm TL and ages 1-4, although I observed fish as old as age 12 and as large as 875 mm TL. Hildebrand and Schroeder (1928) reported a similar size range in the 1920's, 76-838 mm TL (N=280). However, Massmann (1963a) reported most weakfish in the 1950's were < 300 mm TL, with a maximum size of 445 mm TL (N=14,516), and a maximum age of 5.

Current annual age compositions indicate Chesapeake Bay weakfish are fully-recruited to commercial foodfish grades by age 2. Joseph (1972) also reported age 2 as the first age fully-recruited to the Chesapeake Bay pound net catch. However, yearlings sometimes make up a large portion of the commercial catch, as I observed in 1990, and clearly are vulnerable to the gear—especially pound nets and haul seines. Such small, young fish are often sold as scrap and do not show up in commercial foodfish grades. McHugh (1960) found weakfish to be the second most important food fish in scrap from the Chesapeake Bay pound net fishery, and

Massmann (1963a) reported the number of weakfish in pound net scrap often exceeded that in foodfish grades. Thus, although Chesapeake Bay weakfish are fully recruited to foodfish grades at age 2, age at recruitment to pound nets and haul seines is probably younger.

Large, older weakfish occur seasonally in Chesapeake Bay. From 1989 to 1992, older fish (ages 4 and older) were relatively abundant only in April and May. Hildebrand and Schroeder (1928) and Massmann (1963a) also reported seasonal availability of large weakfish in Chesapeake Bay. Although Massmann (1963a) collected few weakfish > 2 lb or age 4 (0.91 Kg), the largest fish in his study (2- and 3-year-olds) were relatively more abundant in April and May, similar to my results. Whereas, Hildebrand and Schroeder (1928) reported weakfish > 3 lbs (1.36 Kg) to be more common in both spring and late fall. Thus, although large fish appear to occur regularly in the spring, their appearance in the fall may be variable.

Age compositions of weakfish in Chesapeake Bay commercial catches are affected by migration. The pattern found in this study—of older fish arriving in Chesapeake Bay in April and May and then apparently leaving approximately when yearlings arrive—was also reported by Nesbit (1954) and Massmann (1963a). This pattern indicates Chesapeake Bay catches, at any one time, do not accurately represent relative abundance at age in Chesapeake Bay. In addition,

some weakfish which spend their younger years in Chesapeake Bay migrate further north as they grow older (Pearson 1932, Nesbit 1954, Perlmutter et al. 1956). It is also unclear if a constant proportion of older fish return to Chesapeake Bay each year. For example, fish ≥ age 4 made up only 4.5% of the 1990 catch but 17.1% and 17.6% of the 1991 and 1992 catches, respectively.

Because weakfish age compositions in Chesapeake Bay are affected by migration, methods of estimating mortality based on age composition, such as catch curve analysis, (Gulland 1983) were not appropriate. These methods are valid only if age compositions are regulated solely by fishing or natural mortality (Vetter 1988). Comparing catch per unit effort of a single year class in successive years also could not be used because older fish are not adequately represented in Chesapeake Bay (Joseph 1972).

It is also difficult to determine weakfish mortality based on maximum ages from one region, as larger and older fish are reported to be more abundant in the northern end of the range (Perlmutter et al. 1956). Thus, a range of probable mortality rates, 0.38-0.77, was calculated based on samples from Chesapeake and Delaware Bays. In comparison, previous estimates of Z have ranged from 0.38 to 1.88 (Vaughan et al. 1991). However, to properly estimate a stock-wide mortality rate, it will be necessary to have year-round catch per unit effort and age/size composition

data, throughout the weakfish range, over several years (Seagraves 1981).

The occurrence of a 17-year-old fish has important implications in terms of weakfish longevity and natural mortality. The maximum age previously reported was age 12 (Shepherd 1988). However, all former maximum ages were based on scales, which underage weakfish older than age 6 (Chapter 1). The 17-year-old was aged as 7 by scales (Villoso 1989)—suggesting older fish may have previously occurred but been underaged. Given the relationship between longevity and natural mortality (Hoenig 1983, Gulland 1983, Vetter 1988), the 17-year-old also suggests weakfish experience lower natural mortality than formerly believed.

Growth

Adult weakfish showed a large range of sizes-at-age and much overlap. Broad size-at-age distributions have been previously reported and attributed to the long spawning season, from May through August (Welsh and Breder 1923, Massmann et al. 1958, Thomas 1971, Chao and Musick 1977). An extended spawning season affects size-at-age in two ways: (1) true age at first annulus deposition varies from 7-12 months, depending on birthdate; and (2) fish born in different months encounter different environments, e.g., temperature, salinity and prey availability, which affect larval growth (Goshorn and Epifanio 1991b) and mortality

rates (Thomas 1971). In addition, spawning pulses could cause several distinct size groups or modes within juvenile size distributions (Massmann et al. 1958, Thomas 1971).

Delaware Bay fish did not demonstrate greater longevity or maximum size than Chesapeake Bay fish in 1992-1993. I found the current maximum age to be 11 in Delaware Bay and 12 in Chesapeake Bay. Maximum size in both regions was 875 mm TL. This is in contrast to Shepherd and Grimes' (1983) hypothesis that weakfish show different regional patterns, with growth and longevity being lowest in the South Atlantic region, intermediate in the Chesapeake Bay region, and highest in Delaware Bay and northward. Shepherd and Grimes (1983) observed a maximum age of 11 in the northern region and 6 in the Chesapeake Bay region. However, their lower maximum age in the Chesapeake Bay region may be due to biased sampling, since their samples for Chesapeake Bay and southward came solely from NMFS trawl surveys—and the ability of large fish to avoid trawls is well-established (Gunderson 1993). In addition, Virginia Saltwater Fishing Tournament data show that over 1,000 fish > 5 Kg were captured in 1980, indicating large fish did occur in the Chesapeake Bay region at the time of Shepherd and Grimes' (1983) study.

Because Delaware Bay fish showed no evidence of greater size-at-age, three Delaware Bay fish ≥ age 8 were included in my von Bertalanffy growth calculations. Even though my

Delaware Bay samples were selected for their large size, only one fish out of 69 had a greater TL-at-age than the size range observed in Chesapeake Bay. Although these results disagree with Shepherd and Grimes' (1983) general conclusion that growth was greatest in the northern region, they are similar to their significance tests of regional size-at-age. They report that northern fish were significantly larger than Chesapeake Bay fish only at age 2, and that Chespeake Bay fish were actually significantly larger than northern fish at age 4. Thus, the older fish from Delaware Bay—rather than showing a different growth pattern—helped fill out the upper half of the von Bertalanffy growth curve for Chesapeake Bay.

Weakfish show similar asymptotic lengths and maximum sizes throughout their range, suggesting they do not demonstrate the regionally-specific growth and longevity proposed by Shepherd and Grimes (1983). My estimate of L_∞ (984 mm TL) for weakfish is comparable to other recent estimates from different regions: 893 mm TL from Delaware Bay (Villoso 1989) and 917 mm fork length (FL) from North Carolina (Hawkins 1988). In contrast, Shepherd and Grimes (1983) reported much lower L_∞ estimates for the Chesapeake Bay region (686 mm TL) and North Carolina (400 mm TL). Their estimates are considerably smaller than the maximum sizes reported for these regions: 875 mm TL for Chesapeake Bay (my study), and 865 mm FL reported for North Carolina

(Hawkins 1988). Additionally, my L_∞ estimate of 984 mm TL is similar to the maximum size reported for Delaware Bay of 960 mm TL (Villoso 1989) and that reported for New York of 950 mm TL (Shepherd 1988).

Differential migration by size is an alternative explanation for the reported higher abundance of large, presumably older weakfish in the northern end of their range (Pearson 1932, Nesbit 1954, Perlmutter et al. 1956). Because swimming speed is a function of body size (Moyle and Cech 1988) larger weakfish would be expected to travel faster and further than smaller fish in a given amount of time. If weakfish constitute a single coastwide stock, as genetic research suggests (Crawford et al. 1988, Graves et al. 1992), and most fish overwinter off North Carolina (Pearson 1932, Hawkins 1988), then larger fish would arrive in northern estuaries before smaller ones in the spring. This is the pattern observed in Chesapeake Bay (Hildebrand and Schroeder 1928, Massmann 1963a, the present study) and Delaware Bay (Feldheim 1975, Villoso 1989). In addition, because larger fish would travel further north, they would be more abundant at the northern end of the weakfish range, thus causing a size-dependent distributional pattern similar to that reported for Atlantic menhaden, Brevoortia tyrannus (Ahrenholz et al. 1987).

The complex spatial and temporal distribution of weakfish, will also affect estimates of seasonal growth.

Growth of temperate water fish usually follows the seasonal cycle, being faster in summer and slower in winter (Moreau 1987), and juvenile weakfish have been shown to grow rapidly during June-September (Mercer 1985). However, mean sizes-at-age for Chesapeake Bay weakfish ages 3-6, were found to be smaller in fall-caught than spring-caught fish in both Nesbit (1954) and this study. This indicates it may not be possible to follow seasonal growth patterns in Chesapeake Bay commercial catches.

Historic trends in maximum size and age

The population structure of Chesapeake Bay weakfish has dramatically fluctuated since the 1920's. Hildebrand and Schroeder (1928) reported most fish in Chesapeake Bay commercial catches weighed from 0.5 lbs to 3 lbs (0.23 Kg to 1.36 Kg), and that 6-10 lb fish (2.72-4.54 Kg) were not uncommon. By the 1950's, however, Massmann (1963a) reported most fish were about 0.25 lbs (0.11 Kg) and few weighed more than 2 lbs (0.91 Kg). Massmann (1963a) concluded the uniformity in size structure from 1954-1958 indicated there were no large fluctuations in year class abundance; rather, that the weakfish population had stabilized at a low level of abundance. In 1970, however, the maximum size and number of large fish began to increase, peaking in 1980. Although the maximum size and number of large fish has recently declined, the current maximum size of 875 mm TL and maximum

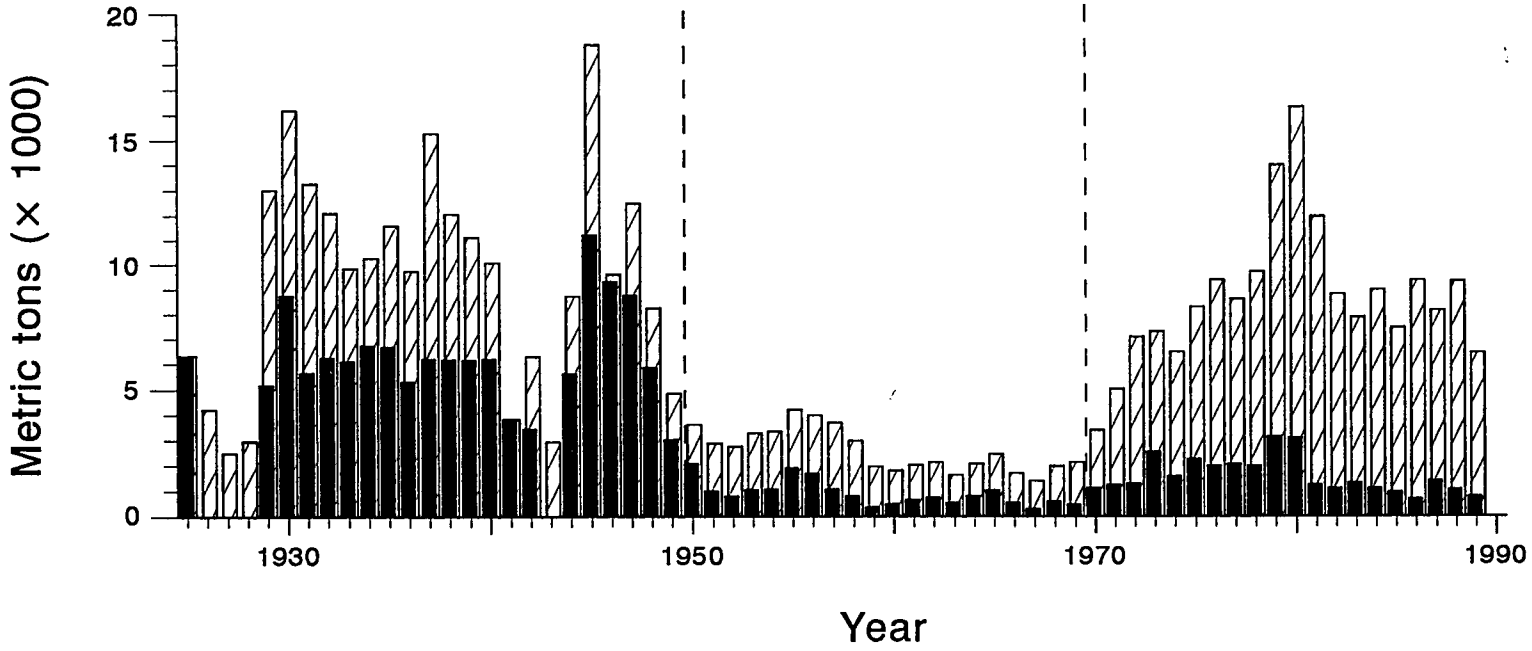
age of 12 remain well-above those reported for the 1950's and 1960's (445 mm TL and age 5) reported by Massmann (1963a) and Joseph (1972).

Similar historic changes in maximum size and age have been reported over much of the weakfish range, with higher maximum ages and sizes during periods of higher landings and presumed abundance (Fig. 23). During the high landings of 1925-1945, the maximum size was 865 mm TL (Nesbit 1954) and maximum age was 8 (Perlmutter et al. 1956). However, during the 1950's and 1960's when landings were low, maximum size decreased to 760 mm TL and the maximum reported age was 6 years (Perlmutter et al. 1956). In the 1970's and 1980's, maximum size and age increased to 960 mm TL (Villoso 1989) and 12 years (Shepherd 1988), concurrent with increased weakfish landings. Because all previous ages were based on scales, the historic pattern of higher maximum ages during periods of higher landings should be valid, even though actual ages may have been underestimated.

An abrupt increase in maximum size and numbers of large weakfish in both Delaware and Chesapeake Bays occurred in 1970 and 1971, respectively. Maximum size steadily rose from 1970 to 1979 and then remained steady until 1989 in both areas. Numbers of increasingly large fish also rose until 1980 in Chesapeake Bay, and 1989 in Delaware Bay. These greater numbers of large, presumably older fish apparently reflect increased recruitment or year-class

Fig. 23. Commercial landings of weakfish coastwide (hatched bars) and in Chesapeake Bay (black bars), 1925-1989, with maximum reported sizes and ages for periods of high and low landings. [a]Nesbit (1954), [b]Perlmutter et al. (1956), [c]Taylor 1916, [d]reported in Seagraves (1981), [e]Massmann (1963a), [f]Merriner (1973), [g]Shepherd (1988), [h]Villoso (1989), [i]present study, [j]Hawkins (1988).

	Before 1950	1950-1969	1970-1993
New York:	Max. TL=865 mm[a] Max. age=8[b]	Max. TL=760 mm[b] Max. age=6[b]	Max. TL=950 mm[g] Max. age=12[g]
Delaware:		Max. TL=392 mm[d] Max. age=4[d]	Max. TL=960 mm[h] Max. age=9[d]
Chesapeake: Bay	Max. TL=720 mm[a]	Max. TL=445 mm[e] Max. age=5[e]	Max. TL=875 mm[i] Max. age=12[i]
North Carolina:	Max. age=8[c]	Max. age=6[f]	Max. age=11[i]



strength, as there is no evidence that fishing mortality decreased. In contrast, effort increased during this same period (Wilk 1981), and higher numbers of young weakfish were being exploited, as peak regional landings shifted to North Carolina where inshore fisheries harvest smaller, younger weakfish than more northern regions (Hawkins 1988).

The increase in large weakfish during the 1970's suggests a series of strong year classes beginning in the late 1960's. The importance of fish born in the late 1960's is indicated by the increase of fish > 1.8 Kg in Chesapeake Bay and > 1.4 Kg in Delaware Bay in 1970 and 1971, respectively. Based on current TGW-at-age data (Table 7), these fish would be 3-4 years-old, on average, and hatched between 1966 and 1968. By 1976, they would be 8-10 years old and average > 5 Kg. The step-wise increase in numbers of fish > 5 Kg in Chesapeake Bay and > 4.6 Kg in Delaware Bay from 1976 to 1980 indicates more fish were growing into this size range than being removed, which would be expected if large numbers of several strong year classes were reaching age 8 or older during this time period.

More than one year-class appears to have contributed to the increase in numbers of large weakfish in the 1970's and 1980's. The pattern in Delaware Bay—of increasing numbers of fish > 4.6 Kg from 1975 to 1980 (Fig. 22), with a decrease in 1981 and 1982 and then a second increase until 1986—suggests the contribution of more than one year class.

It is also unlikely that the more than 1,300 fish > 5.0 Kg recorded in Delaware Bay in 1987 were solely from the late 1960's year classes, since they would then be 19-21 years-old.

The factors which produced the large year-classes, and allowed large numbers of weakfish to survive to older ages, are not clear. Joseph (1972) suggested reproductive failure as the cause of the low landings in the 1950's and 1960's, and thus increased reproductive output in the late 1960's could have caused increased year-class strength (see Chapter 3). However, the index of juvenile weakfish abundance, based on trawl surveys of the York River, VA, 1955-1982, showed only a small increase in abundance in 1968—which did not exceed levels in the 1950's—a larger peak in 1970, and an extreme peak in 1980 (Mercer 1985). Thus, increased recruitment by itself may not explain fluctuations in weakfish landings and maximum age.

However, under the right circumstances, even a small increase in recruitment, such as that seen in 1968, could have a large effect on year-class strength. At low population levels, density dependent factors such as cannibalism, competition, and food availability should have less of a negative impact on abundance (Hilborn and Walters 1992). In addition, factors such as increased food availability, which would increase reproductive output (Houde 1989), would also be expected to decrease adult

natural mortality rates.

Thus, slightly increased recruitment with improved food resources and less competition/predation may better explain the historical trends. The large increase in maximum age from approximately age 6 in the 1950's/1960's to at least age 12 in the 1970's/early 1980's suggests a change in mortality rates. Based on the reasoning of Royce (1972) these ages correspond to instantaneous mortality rates, Z, of 0.77 for age 6, and almost half that, 0.38, for age 12. Given the equation: $Z = M + F$, where M=instantaneous natural mortality rate, and F=instantaneous fishing mortality rate (Ricker 1975), either M or F or both must have decreased during the 1970's for Z to have decreased. Since fishing pressure is reported to have increased during this time, the lower mortality rates must be due to a decrease in natural mortality (M). Such fluctuations in M are not uncommon, and can be caused by numerous factors, including food supply and predation (Vetter 1988, Hilborn and Walters 1992). In 1970/1971, the population of Atlantic menhaden—a major food source for weakfish > 250-300 mm TL (Welsh and Breder 1923)—also began to increase, after a period of decreased stock size in the 1960's (Ahrenholz et al. 1987). Whereas, striped bass—a weakfish competitor and predator (Mercer 1985)—began a period of decreased recruitment in Chesapeake Bay from 1971-1980 (Houde and Rutherford 1993) and below-average landings beginning in 1975 (Rothschild et al. 1981).

Future research is necessary to better understand fluctuations in year-class strength and interactions between weakfish and other species. Stock-wide mortality rates need to be estimated and weakfish migration better understood. It is especially important that ages be based on sectioned otoliths—a validated ageing technique—so that future estimates of growth parameters, mortality and longevity can be better compared over time and space.

CHAPTER 3

Reproductive biology

INTRODUCTION

The reproductive biology of weakfish is not well understood. Aspects of weakfish reproductive biology have been reported by many authors (e.g. Welsh and Breder 1923, Hildebrand and Schroeder 1928, Hildebrand and Cable 1934, Pearson 1941) and more recently, several studies on weakfish reproduction have been published (Merriner 1976, Shepherd and Grimes 1984, Villoso 1989). All these studies reported an extended spawning season, suggestive of a multiple spawner. However, descriptions of the weakfish spawning pattern are contradictory. Merriner (1976) suggested weakfish were multiple spawners in North Carolina waters, but Shepherd and Grimes (1984) found no evidence of this at the northern end of the range. Villoso (1989) observed multiple spawning in hormonally-injected weakfish in the laboratory and concluded from oocyte diameter distributions that weakfish in Delaware Bay spawn more than once each season, possibly 2-4 times. No study has considered the possibility of indeterminate fecundity (Hunter and Macewicz 1985), or how it would affect the validity of previous fecundity estimates. There is no information on spawning

frequency. Moreover, weakfish reproduction has not been studied in Chesapeake Bay, an apparently important spawning ground (Higgins and Pearson 1928, Merriner 1973, Olney 1983).

This study describes in detail weakfish reproductive biology in the Chesapeake Bay region, emphasizing determination of the spawning pattern (i.e., multiple versus total), and the type of fecundity (i.e., indeterminate or determinate). Size and age at first maturity, sex ratios, spawning periodicity, batch fecundity, spawning frequency, diel periodicity of spawning and the relative asynchronicity of the spawning population are assessed. How these factors affect annual egg production and its variation are also evaluated.

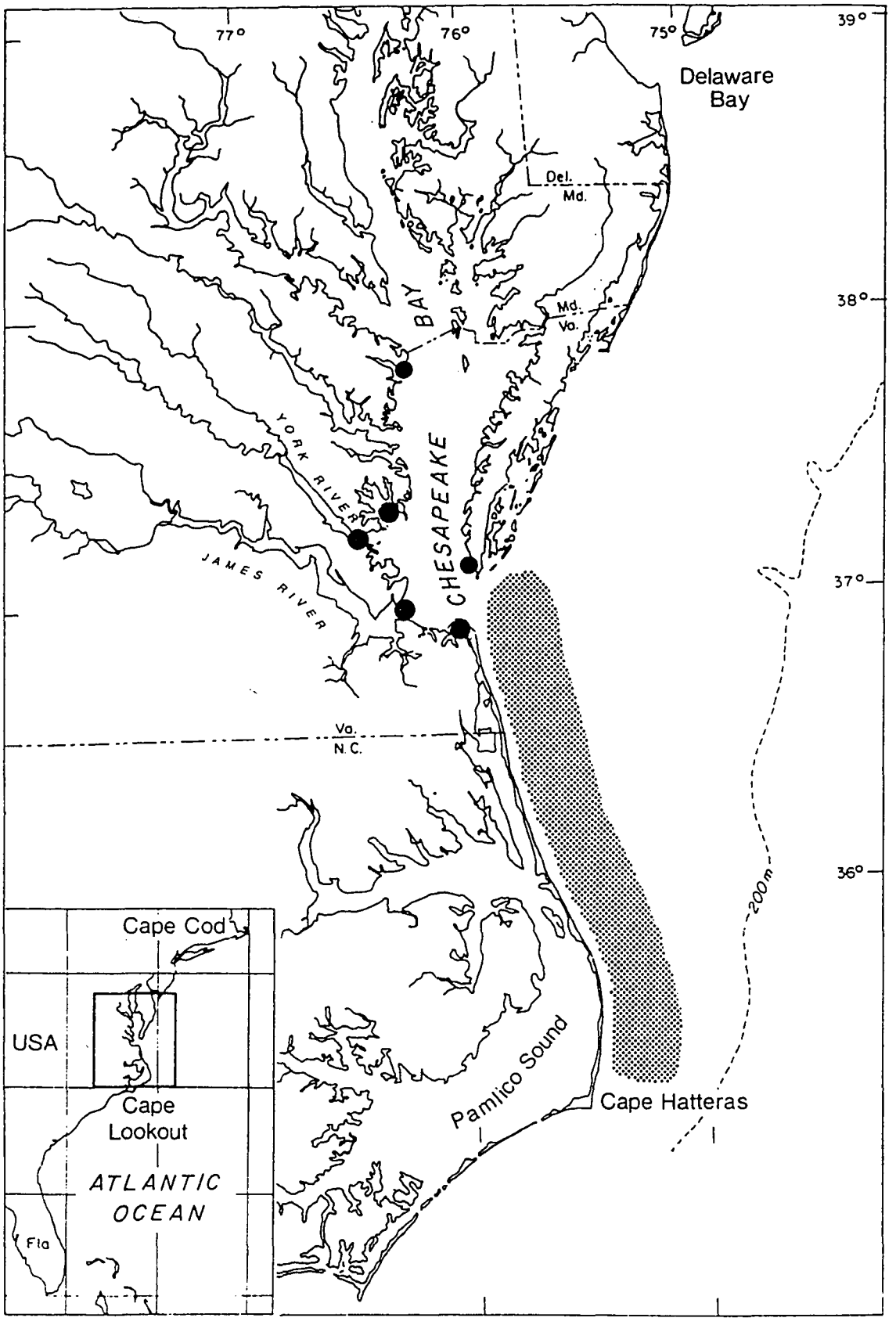
MATERIAL AND METHODS

Collection of samples

A total of 4,380 weakfish were collected from commercial fisheries in 1989-1992. In 1989, collections were made during the fishing season from pound net fisheries in the Chesapeake bay every other week (Fig. 24). One 22.7 Kg (50-lb) box of fish of each available market grade (small, medium or large) was purchased and processed for general biological data.

From 1990 to 1992, weakfish were collected weekly for general biological data, primarily from gill net and haul seine fisheries on the western shore of the lower Bay (Fig. 24). These samples were supplemented during the winter with monthly samples from commercial trawlers operating in Virginia and North Carolina shelf waters (Fig. 24), where weakfish are believed to overwinter (Pearson 1932, Wilk 1979). In 1991, additional morning and evening samples were collected daily from gill nets in the lower York River over the May-August spawning period to determine diel periodicity, and to collect hydrated females to estimate batch fecundity and spawning frequency. Fish alive when the

Fig. 24. The Chesapeake Bay region. Black dots indicate pound net, haul seine or gill net collection sites and the hatched area indicates where otter trawl collections were made.


77°
76°
75°
39°
38°
37°
36°
Delaware Bay
Del.
Md.
Md.
Va.
CHESAPEAKE BAY
YORK RIVER
JAMES RIVER
Va.
N.C.
200m
Pamlico Sound
Cape Hatteras
Cape Cod
USA
Cape Lookout
ATLANTIC OCEAN
Fla

nets were emptied (0600-2030 hrs) were marked, and their kill-times and orientation (i.e., caught moving inshore or offshore) recorded. In 1991, to supplement diel periodicity data, fish were also collected with hook and line and their kill times recorded (2100-2400 hrs).

In 1992, evening samples (1650-2030 hrs) were collected weekly from May-August using the same gill nets on the lower York River to estimate spawning frequency and batch fecundity. Fortnightly samples were also collected from May-August from a haul seine fishery in the lower York River for histological estimates of spawning frequency. In an attempt to collect older gravid females, the gonads of 34 fish collected in May from the 1992 World Championship Weakfish Tournament in Dover, DE were examined and batch fecundity was estimated for one gravid female. In 1991 and 1992, an additional 160 fish, 140-275 mm total length (TL), were sampled from the VIMS juvenile trawl survey to supplement commercial samples for size and age at maturity data—because commercial fisheries have a minimum size limit of 9" or 229 mm TL. Details on sampling design and gear of the VIMS survey can be found in Chittenden (1989a) and Geer et al. (1990).

General biological data

Total length (TL) was measured to the nearest millimeter and total gutted weight (TGW) was determined to

the nearest gram. Gutted weights were used because weakfish are piscivorous and can swallow fish a third of their own weight, which would greatly bias somatic weights (SW). Gonads were then removed, sexes recorded and gonad weight (GW) determined to the nearest gram. Detailed notes of the whole gonad appearance were recorded and photographs taken of representative stages to later verify macroscopic gonad staging. Macroscopic gonad stages were assigned to females as outlined in Table 11. Males were classified only as mature or immature, because a finer breakdown of male gonad stages is difficult and subjective. The gonadosomatic index (GSI) was calculated as (GW/SW) x 100. Ages were determined by thin-sectioned otoliths (Chapter 1) for 3,245 of the fish sampled.

Microscopic gonad analysis

Spawning pattern and type of fecundity were assessed by oocyte diameter distributions (Hunter and Macewicz 1985, West 1990), microscopic whole oocyte analysis (Clark 1934, Forberg 1983, West 1990) and histology (Hunter and Macewicz 1985). Measurements for oocyte diameter distributions were made on oocyte samples that had been hydraulically separated from the ovary and each other and preserved in 2% formalin, using the method of Lowerre-Barbieri and Barbieri (1993). Samples were stirred before oocytes were removed to reduce bias due to settling differences, and 500 oocytes were

Table 11. Description of gonad maturity stages for female weakfish in the Chesapeake Bay region. Macroscopic appearance refers to fresh ovaries. FOM = final oocyte maturation; GSI = gonadosomatic index; POFs = postovulatory follicles.

Stage	Macroscopic appearance	Microscopic appearance
(1) Immature	Ovaries very small, translucent, ribbon-like (GSI<1.00).	Only primary growth oocytes present; no atresia; ovarian membrane thin.
(2) Developing	Ovaries ranging from small to medium (≤ 25% of body cavity); light orange in color; no opaque (advanced yolked) oocytes present (mean GSI=1.81).	Only primary growth, cortical alveoli and a few partially yolked oocytes present; there may be atresia.
(3) Fully-developed	Ovaries large (50-75% of body cavity); pale yellow in color; opaque oocytes prevalent and easily detected; little ovarian vascularization and no signs of previous spawning (mean GSI=7.04).	Primary growth to advanced yolked oocytes present; may be atresia of advanced yolked oocytes; no remnant hydrated oocytes or POFs.
(4) Gravid	Ovaries ranging from medium to very large (25-100% of body cavity); clear (hydrated) oocytes visible amongst opaque oocytes, giving a speckled appearance; late in the season, ovaries may be smaller and reddish due to an increase in the ratio of clear to opaque oocytes and ovarian vascularization (mean GSI=15.48).	Primary growth to FOM/hydrated oocytes present; often major atresia of advanced yolked oocytes; hydrated oocytes are unovulated. Remnant hydrated oocytes from a previous spawn or degenerating POFs may be present.
(5) Running-ripe	Ovaries ranging from medium to large (25-75% of body cavity); clear oocytes have been ovulated and are visible as a collective clear strip amongst the yolked oocytes; some may have been extruded; occasionally no opaque oocytes present (mean GSI=12.70).	Primary growth to ovulated, hydrated oocytes and POFs present; often major atresia of advanced yolked oocytes; occasionally only hydrated and primary growth oocytes present.
(3') Partially-spent/ Redeveloping	Ovaries somewhat flaccid, ranging from medium to small (≤ 30% of the body cavity); orangish in color due to increased ovarian vascularization. Often a 'ridge' (a red area along the dorsal ovarian edge) is present. Remnant hydrated oocytes may occur in the 'ridge' or at the posterior end of the ovaries (mean GSI=6.63).	Primary growth to advanced yolked oocytes present; often remnant hydrated oocytes and POFs present. May be atresia of advanced yolked oocytes. Similar to stage 3.
(6) Regressing	Ovaries quite flaccid and small (< 20% of body cavity); mustard yellow to orange, occasionally maroon; often contain clear fluid; can detect a few opaque oocytes (mean GSI=1.38).	Primary growth and cortical alveoli oocytes present; yolked oocytes being resorbed. May be remnant hydrated oocytes or degenerating POFs.
(7) Resting	Ovaries very small; dark orange to maroon in color; no opaque oocytes present; ovarian membrane thickened and more opaque than in immature fish (mean GSI=0.82).	Most oocytes (> 90%) are primary growth; may have other oocytes in late stages of atresia; more follicular tissue than immature fish.

measured from each ovary. Measurements were made with an ocular micrometer in a dissecting microscope along the median axis of the oocyte parallel to the horizontal micrometer gradations (Macer 1974, DeMartini and Fountain 1981).

To evaluate the occurrence of remnant hydrated oocytes and to compare whole oocyte appearance with histological appearance, whole oocytes were microscopically analyzed for all gravid females used for batch fecundity estimates and a random subsample of 25% of all ovaries macroscopically staged as partially-spent/redeveloping in 1991 (Table 11). Fresh oocyte samples from ovaries macroscopically staged as partially-spent/redeveloping were removed from the right ovary, spread on a microscope slide and examined under a dissecting microscope (12-50x). The incidence of remnant hydrated oocytes, indicating recent spawning, was recorded as well as the general appearance of yolked oocytes (i.e., whether most yolked oocytes appeared healthy or not). Oocyte diameters were measured for 20 of the most developed oocytes in the ovary. Representative fresh oocyte samples were also photographed for later comparison to histological slides from the same fish. Microscopic analysis of oocyte samples from gravid females was carried out in the same way and the mean diameter of 20 fresh, unovulated hydrated oocytes was calculated.

Histological samples were collected from June-September

1990, January-December 1991, and March-September 1992 to verify macroscopic gonad staging, assign developmental stages to oocyte size-frequency distributions and to determine the relative amount and frequency of atresia. For histological preparation, tissue samples were fixed in 10% neutrally-buffered formalin for 24 hrs, soaked in water another 24 hrs, and stored in 70% ethanol. Samples were then embedded in paraffin, sectioned to 5-6 μm thickness and stained with Harris' Hematoxylin and Eosin Y.

Histological classification was based on five developmental oocyte stages: primary growth, cortical alveoli, partially-yolked, advanced yolked, and final oocyte maturation (FOM)/hydration (Wallace and Selman 1981, Hunter et al. 1992). Advanced yolked oocytes were further broken down into early or late stages, based on the coalescence of oil droplets and oocyte diameter, similar to Matsuyama et al.'s (1990) secondary and tertiary yolked stages. The presence of postovulatory follicles (POFs) was noted, and POFs were aged for fish with known kill-times. POF ages were calculated following the reasoning of Alheit et al. (1984) by determining the time elapsed since the time of peak spawning activity, which was determined to be dusk (see Diel Periodicity section in Results). Only fish with known kill times were used for histological analysis of atresia (N=234), so that atretic oocytes would not be confused with post-mortem effects.

The concurrent presence of oocytes at all stages of development in fully-developed and partially-spent ovaries and the lack of distinct modes or gaps in oocyte diameter distributions, except in gravid or running-ripe ovaries, was considered to indicate asynchronous oocyte development and indeterminate fecundity (Wallace and Selman 1981, Hunter and Macewicz 1985).

Sex ratio

Monthly sex ratios in 1990-1992 were tested using a χ^2 test for significant differences from an expected 1:1 ratio. A χ^2 test was also used to test for significant differences in sex ratios by gear (haul seine and gill net) from the overall observed sex ratio of 3:1.

Size and age at maturity

Size at maturity estimates were based on 817 females and 394 males, 153-310 mm TL. Females were considered mature if their ovaries contained yolked oocytes, i.e. were in the fully-developed stage (Table 11). Males were considered mature if milt was observed in the lumen after cutting the testes transversely. To avoid classifying resting fish as immature, these samples were collected during May, June and July, when resting, mature fish are rare (see Spawning season/location in Results). Mean TL at

first maturity (L_{50}) was estimated by fitting the fraction of mature fish per 10 mm TL intervals to the logistic function by nonlinear regression (Marquardt method), using FISHPARM (Saila et al. 1988). L_{50} was defined as the smallest predicted length interval in which 50% of the individuals were mature.

An additional 48 age 1 females, 165-322 mm TL, were histologically examined to determine if fish in this size and age range were actually spawning or developing yolked oocytes which would later be resorbed before spawning occurred (Forberg 1983). The presence of hydrated oocytes and POFs was recorded, as they indicate either imminent or recent spawning activity (Hunter and Macewicz 1985).

Age composition of spawning population

Age composition of the spawning population was assessed by evaluating macroscopic and histological ovarian stages by age over the spawning season. Spawning activity was delineated by: (1) the pattern of mean weekly GSIs of non-hydrated females, (i.e., excluding gravid and running-ripe females); (2) the percentage of gravid and running-ripe females collected over the spawning season; and (3) the monthly percentages of each macroscopic gonad stage. The periodicity of females with gonad stages 4 & 5 or FOM/POFs in histological slides—signifying fish about to spawn or which had just recently spawned (see Diel Periodicity

section in Results)—was considered to indicate duration of the spawning season (West 1990).

Spawning activity

Effects of the lunar cycle, water temperature and food availability/body condition on spawning activity were also assessed. Water temperatures in 1990-1992 were taken 1.5 m below the surface in water approximately 4 m deep at the mouth of the York River. Food availability was assessed by evaluating gut fullness. Guts were considered empty if they were devoid of food and full if they at least contained partially-digested remains. Fulton's condition factor, K, was used to express body condition (Ricker 1975) for age 2 and 3 fish in 1991 and 1992, because these ages were most abundant in the Chesapeake Bay weakfish spawning population (See Age Composition of the Spawning Population section in Results).

Batch fecundity

Batch fecundity was estimated gravimetrically (Bagenal and Braum 1978), using the hydrated oocyte method (Hunter et al. 1985) on fresh ovarian samples. In 1991, 50 gravid females were used to assess within and between-ovary positional effects on abundance of hydrated oocytes, as well as to estimate batch fecundity. Four 0.2 g ovarian

subsamples were collected from each pair of ovaries: one each from the anterior, middle and posterior sections of the right ovary, and one from the middle of the left ovary. A one-way analysis of variance (ANOVA) was used to evaluate positional effects within and between ovaries. All hydrated oocytes were counted in each subsample under a dissecting microscope at a magnification of 24x. In 1992, after finding no positional effects, batch fecundities were estimated from two 0.1 g subsamples taken from the right ovary. The relationships of batch and relative fecundity (relative fecundity=batch fecundity/SW) to TL and SW were assessed with simple linear regression, as were relationships of relative fecundity and egg diameter over the spawning season.

Spawning frequency

Spawning frequency was estimated by the POF method (Hunter and Goldberg 1980, Hunter and Macewicz 1985) and by the hydrated oocyte method (DeMartini and Fountain 1981, Hunter and Macewicz 1985).

Annual fecundity

Annual fecundity was estimated as the number of spawns per female times the mean annual batch fecundity. The number of spawns per female was estimated by dividing the

number of days in the spawning season by the estimated annual spawning frequency.

Statistical analysis

All data were analyzed using statistical methods available through the Statistical Analysis System (SAS 1988). Assumptions of linear models were checked by residual plots as described in Draper and Smith (1981).

RESULTS

Spawning season/location

Weakfish spawn over an extended spawning season, May-August, although some fish continue to spawn until mid-September. Mean monthly GSIs for both males and females were low during January-March (≤ 1 for males and < 2 for females), increased in April, peaked in either May or June, and returned to low pre-season levels by September (Fig. 25). This same temporal pattern was seen in ovarian maturity stages. In 1991 and 1992, all females were developing by April and some began to spawn in May (Fig. 26). Spawning (gravid and running-ripe) females occurred from May-August, and by September most females had regressing ovaries. However, some spawning may continue in early September, as two females with POFs were collected in September 1990 (see Spawning Pattern section).

Weakfish population gonad development and initiation of spawning is synchronous, whereas cessation of spawning is asynchronous. All females examined histologically in January-April had begun to develop and had at least primary growth and cortical alveolar oocytes present. The first

Fig. 25. Mean monthly gonadosomatic index and range of mature male and female weakfish in the Chesapeake Bay region 1990-1992. N=sample size.

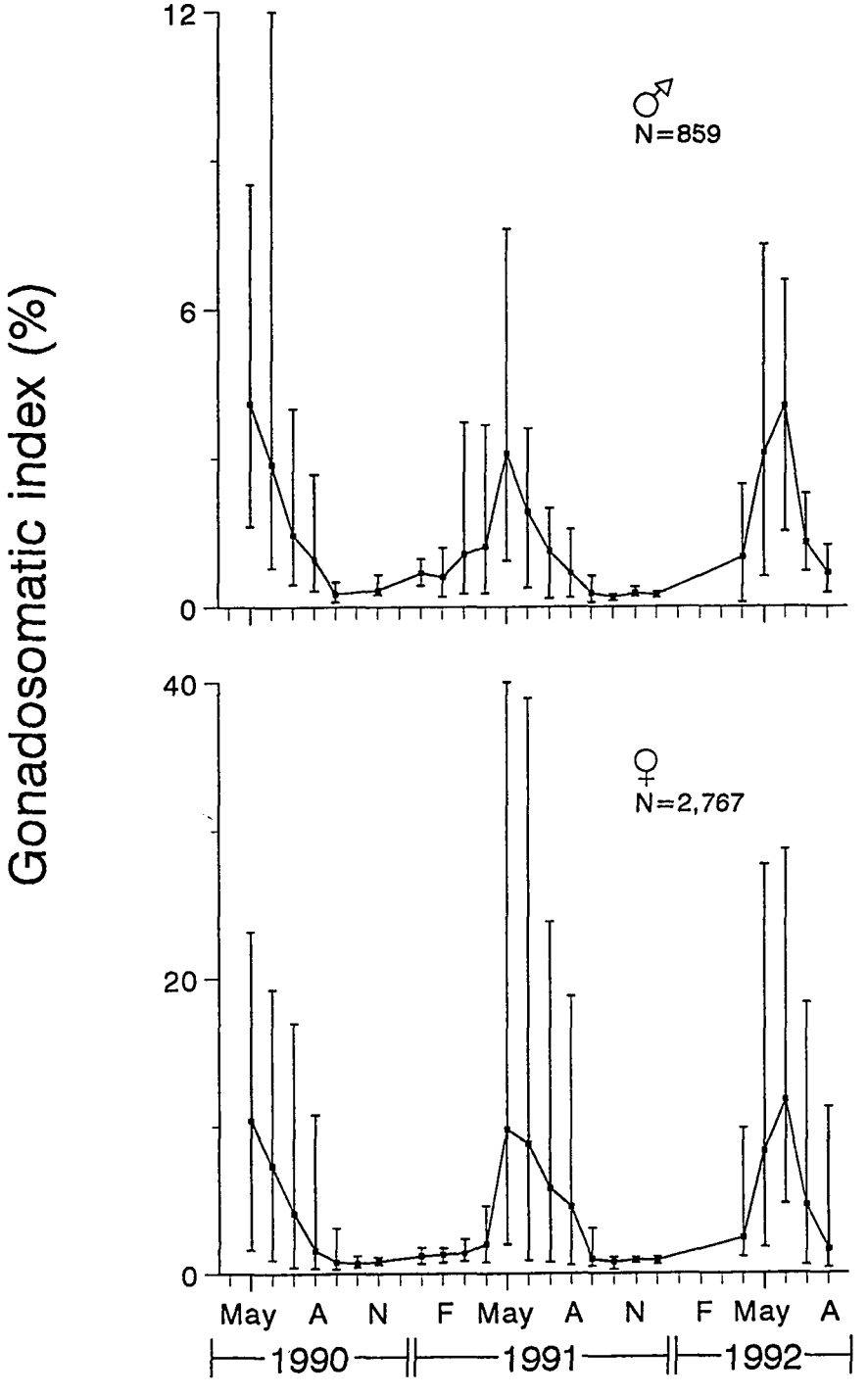
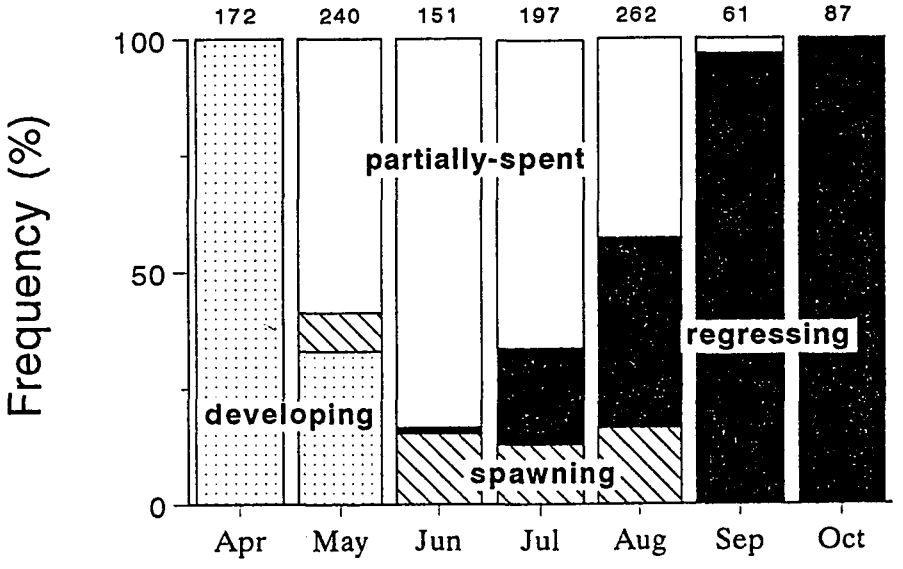

Gonadosomatic index (%)
12
6
0
♂
N=859
40
20
0
♀
N=2,767
May
A
N
F
May
A
N
F
May
A
1990
1991
1992
Date

Fig. 26. Frequency of different reproductive phases for mature, female weakfish in the Chesapeake Bay region, 1991-1992. Monthly sample sizes are noted above the bars. Reproductive phases indicated in the graph consist of the following macroscopic gonad stages:developing=developing+fully-developed; spawning=gravid+running-ripe; partially-spent= partially-spent; and regressing=regressing+resting.


172
240
151
197
262
61
87
100
50
0
Frequency (%)
partially-spent
regressing
developing
spawning
Apr
May
Jun
Jul
Aug
Sep
Oct

signs of yolking usually occurred in mid-April. By May, all mature females had advanced yolked oocytes and were capable of spawning, indicating a synchronous initiation of spawning. However, cessation of spawning was asynchronous as indicated by occasional females with regressing ovaries as early as June, while other females continued to have partially-spent ovaries until mid-September.

Weakfish spawn in Chesapeake Bay from approximately mid-May through August. A large number of spawning females (N=134) were collected in Chesapeake Bay from 1990-1992. Of these females, 114 were gravid and 20 were running-ripe, i.e., actually in the process of spawning when caught. However, gravid females can also be considered active spawners, because ovulation and subsequent spawning is rapid (see Diel Periodicity section). Fully-developed and partially-spent females were collected from all locations in Chesapeake Bay, as were males with flowing milt (Fig. 24). Additionally, two gravid and three running-ripe females occurred at my most northern collection site, just below the Maryland/Virginia border (Fig. 24), indicating weakfish are capable of spawning well-within the Bay mouth. Spawning females first occurred in Chesapeake Bay in May—during the 3rd week in 1990 and 1991 and the 1st week in 1992—and were present each year until the last week of August. Males with flowing milt were also collected from mid-May through August.

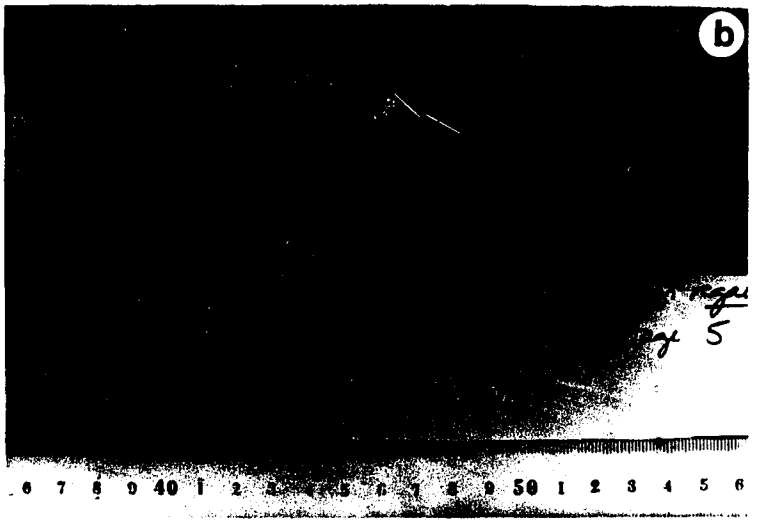
Spawning pattern

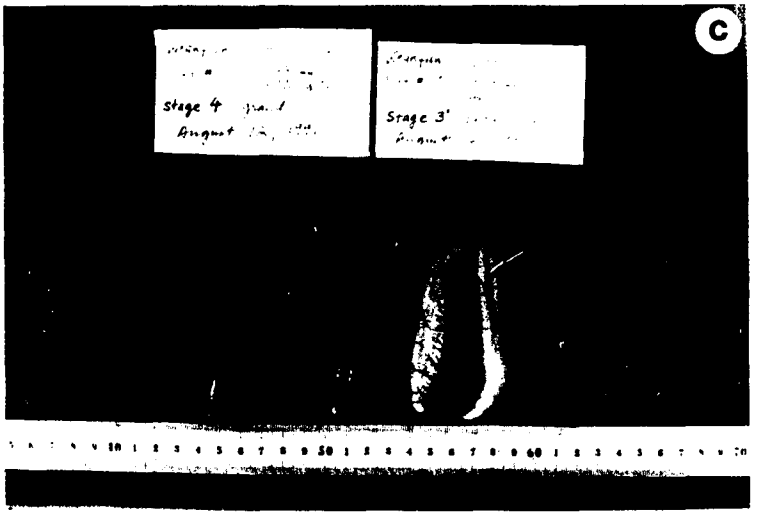
Four lines of evidence indicate weakfish are multiple spawners in the Chesapeake Bay region: 1) the appearance and incidence of ovarian maturity stages; 2) the regular occurrence of remnant hydrated oocytes in partially-spent /redeveloping ovaries; 3) the oocyte development and fecundity pattern; and 4) the occurrence of POFs in ovaries containing healthy yolked oocytes.

The macroscopic ovarian maturity stages in weakfish (Table 11) are typical of a multiple spawner. Weakfish hydrate and spawn only a small portion of the oocytes within their ovaries in each spawning event, as evidenced by the speckled appearance of gravid ovaries early in the season when relatively few translucent, hydrated oocytes are interspersed amongst many opaque, yolked oocytes (Fig. 27a). Three gravid females collected from Delaware Bay on May 28, 1992 demonstrated the same speckled ovarian appearance. That weakfish hydrate and spawn only a small portion of their oocytes for each spawning event is also indicated by the clear streaks of ovulated hydrated oocytes surrounded by opaque yolked oocytes in running-ripe ovaries (Fig. 27b). Although gravid ovaries changed in appearance as the spawning season progressed, showing a higher ratio of hydrated to yolked oocytes and increased vascularization, both yolked and hydrated oocytes continued to be present (Fig 27c). Partially-spent/redeveloping ovaries were common

Fig. 27. Examples of different ovarian stages in weakfish: (a) gravid, early in the season, GSI=23.4, note speckled appearance of hydrated oocytes; (b) running-ripe, GSI=10.4, arrow indicates the clear stripe of ovulated, hydrated oocytes; and (c) late in the season highly-vascularized gravid, GSI=11.7 (left) and partially-spent, GSI=4.9 (right), arrow indicates the 'ridge'.

a





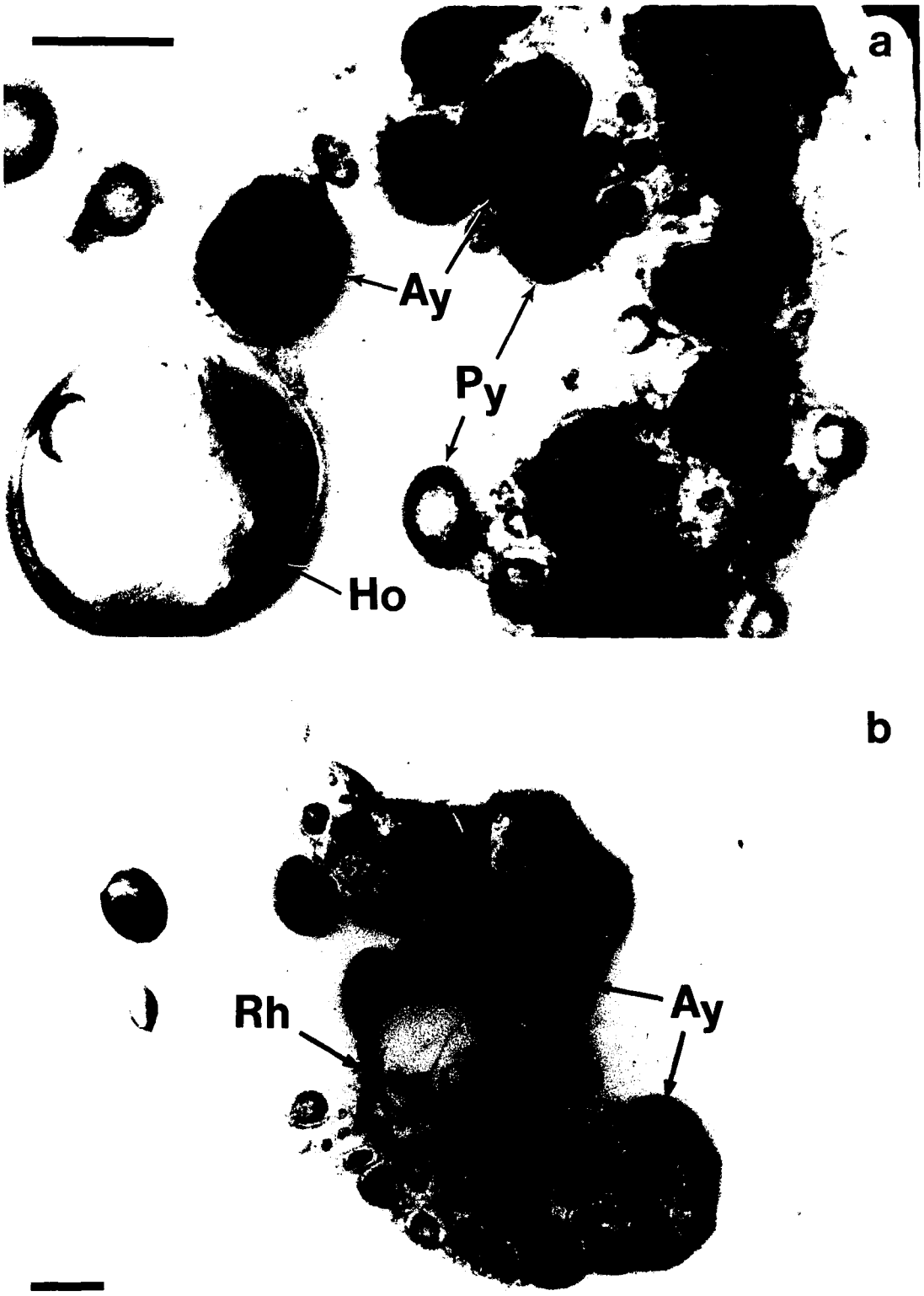
and characterized by a highly-vascularized 'ridge' area, where ovulated hydrated oocytes had collected prior to spawning (Fig. 27c).

The incidence and duration of weakfish ovarian maturity stages also indicate a multiple spawner. Spawning females, (e.g., gravid and running-ripe), were collected throughout the May-August spawning period (Fig. 26). However, most (> 50%) females did not finish spawning—as indicated by regressing ovaries—until September, suggesting a pattern of repeat spawns.

Remnant hydrated oocytes were regularly observed in partially-spent/redeveloping weakfish ovaries, also typical of a multiple spawner. Because weakfish, like other multiple spawners, hydrate and spawn only a small portion of the total oocytes present in their ovaries, gravid ovaries contain fully-hydrated, unovulated oocytes, surrounded by less-developed oocytes (Fig. 28a). The relatively small number of hydrated oocytes, surrounded by large numbers of less-developed oocytes, often leads to a lack of all hydrated oocytes being extruded during spawning. The occurrence of remnant hydrated oocytes in good condition from partially-spent/redeveloping weakfish ovaries indicated fish which had recently spawned, and were capable of continued spawning—as evidenced by the presence of healthy advanced yolked oocytes (Fig. 28b).

The oocyte development and fecundity pattern of

Fig. 28. Whole weakfish oocytes from: (a) the gravid ovary in Fig. 26c, GSI=11.7; and (b) a partially-spent ovary, from a fish that died at 7 A.M., GSI=2.3. Bar=500 μm; Ay=advanced yolked oocyte; Py= partially yolked oocyte; Ho=hydrated oocyte; Rh=remnant hydrated oocyte.


a
Ay
Py
Ho
b
Rh
Ay

weakfish were also characteristic of multiple spawners. The presence of oocytes in all developmental stages in fully-developed and partially-spent ovaries (Fig. 29a and b) indicated that weakfish have asynchronous oocyte development. Because the relative abundance of different oocyte types appeared quite different in histological slides than from preserved, whole oocytes (comparison of Fig. 29a and Fig. 30 top, which are from the same ovary), oocyte diameter distributions were based on whole oocyte samples. Oocyte samples showed a typical diameter size range for each developmental stage: 0.01-0.14 mm for primary growth, 0.15-0.31 mm for cortical alveoli, and 0.32-0.55 mm for yolked oocytes (partially-yolked and advanced yolked). However, there was much overlap and no distinct modes (Fig. 30). The only gaps in weakfish oocyte diameter distributions occurred between hydrated and yolked oocytes, indicating weakfish have indeterminate fecundity.

The common occurrence of POFs in partially-spent/redeveloping ovaries also indicated a multiple spawner. In general, ovaries containing POFs also contained healthy, early advanced yolked oocytes (Fig. 29b), signifying that they had recently spawned and were capable of spawning again.

Sex Ratios

More female than male weakfish occurred in Chesapeake

Fig. 29. Histological appearance of weakfish oocytes. (a) Oocytes from a fully-developed ovary, with primary growth (Pg), cortical alveoli (Ca), partially-yolked (Py), and advanced yolked (Ay) oocytes. Note both early-stage advanced yolked (upper left) and late-stage advanced yolked oocytes (bottom right). Bar=500 μm. (b) Oocytes from a partially-spent ovary with degenerating POFs (Dp) and the next batch of early-stage advanced yolked oocytes (Ay). Bar=250 μm.

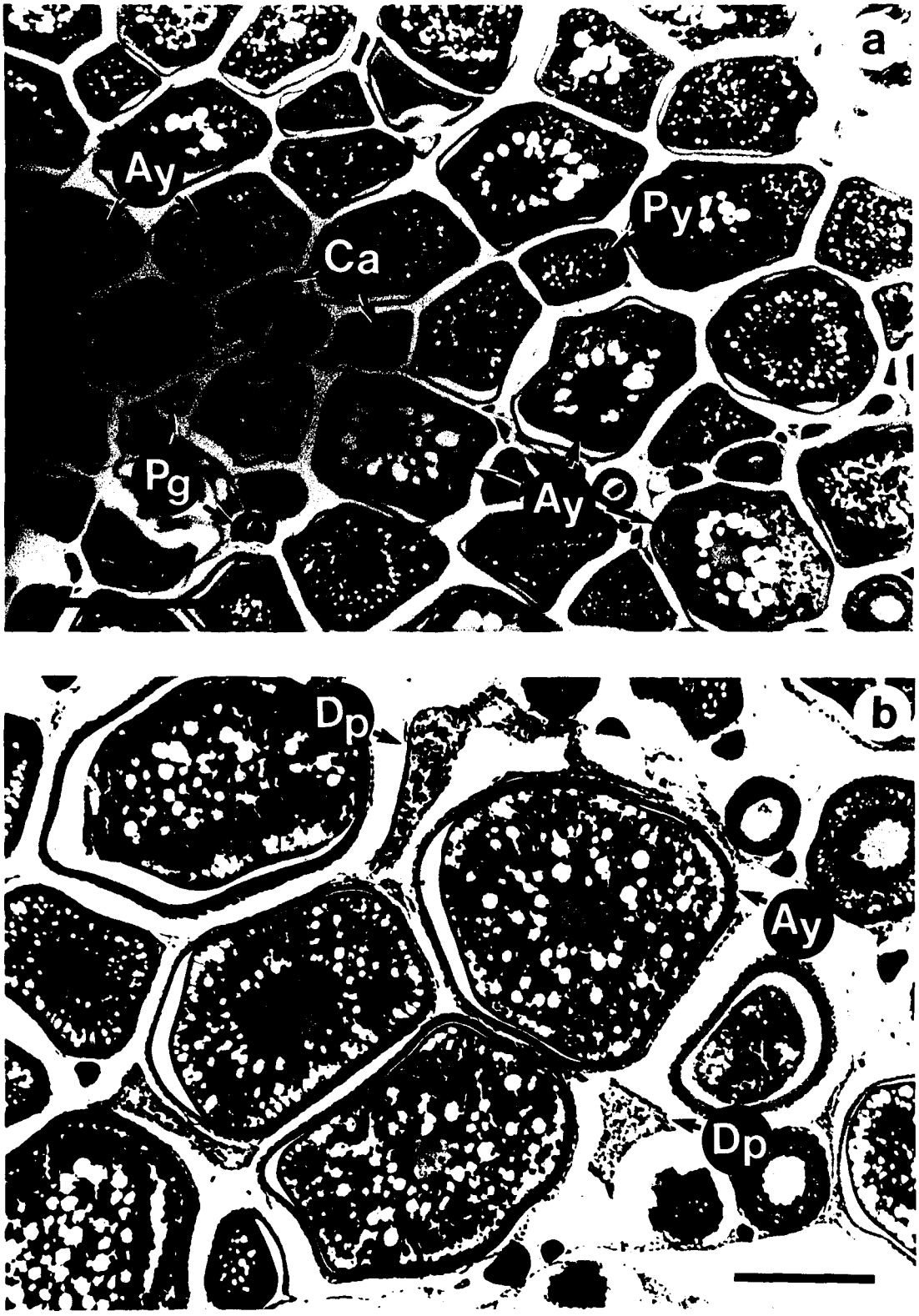
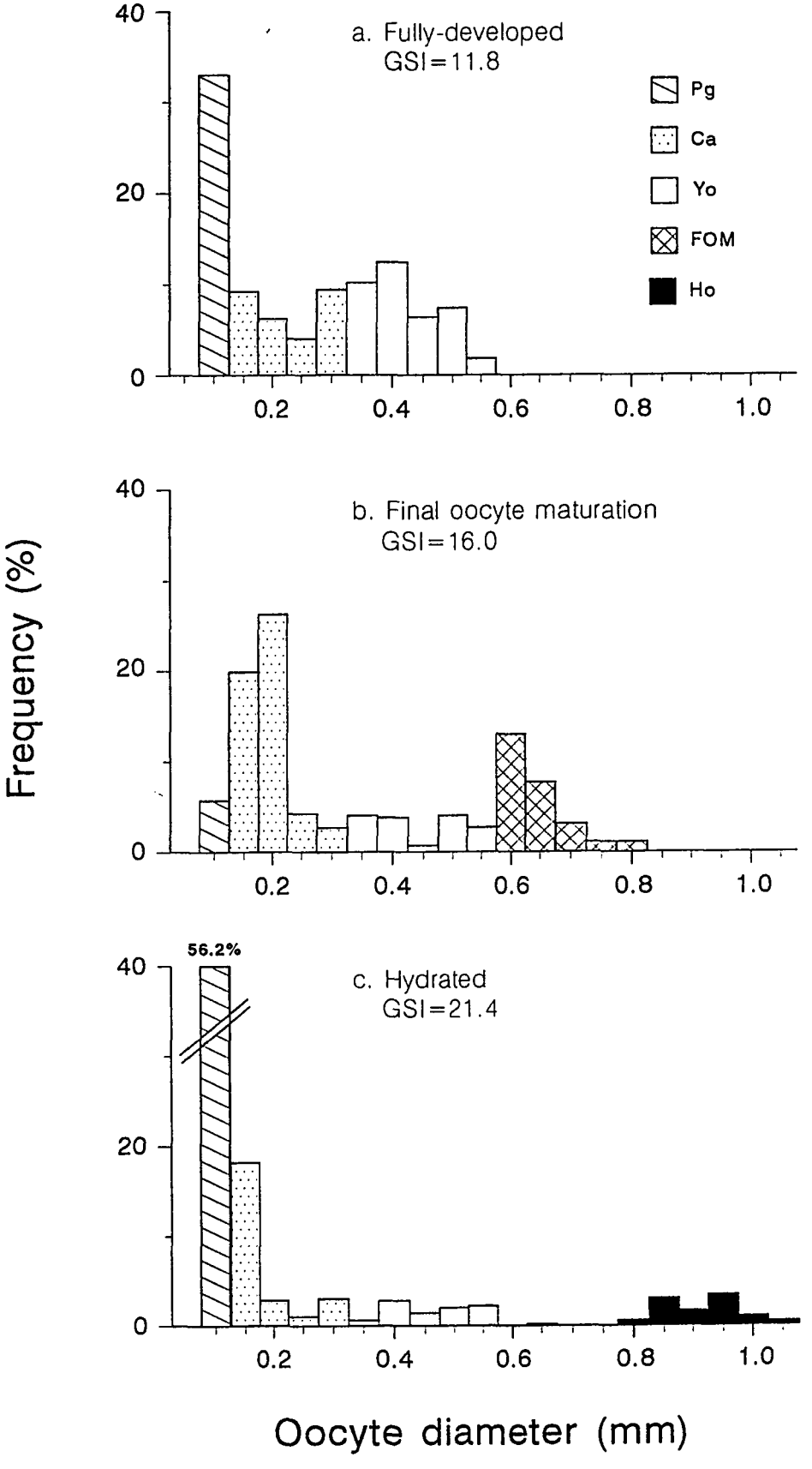

a
Ay
Ca
Py
Pg
Ay
b
Dp
Ay
Dp

Fig. 30. Oocyte diameter distributions from different stage weakfish ovaries: (a) the fully-developed ovary depicted in Fig. 29a; (b) an ovary which has begun final oocyte maturation (FOM); and (c) an ovary containing fully-hydrated, unovulated oocytes. Pg=primary growth, Ca=cortical alveoli, Yo=yolked (both partially- and advanced-yolked), FOM=final oocyte maturation, Ho=hydrated oocytes. The progression, a to c represents oocyte development from dawn to dusk, the day of a spawn.


a. Fully-developed
GSI=11.8
Pg
Ca
Yo
FOM
Ho
b. Final oocyte maturation
GSI=16.0
c. Hydrated
GSI=21.4
56.2%
40
20
0
0.2
0.4
0.6
0.8
1.0
Frequency (%)
Oocyte diameter (mm)

Bay. Overall sex ratios each year were approximately 3:1 females to males (Fig. 31). Monthly sex ratios in Chesapeake Bay were consistently skewed towards females from June-October, but did not significantly differ from an expected 1:1 ratio in some spring and fall months, when weakfish migrate (Table 12). Sex ratios from different gears did not differ significantly from the overall observed ratio of 3:1 (Table 13). In contrast, winter (November-February) samples from North Carolina shelf waters in 1991 showed no significant difference from an expected 1:1 ratio (Fig. 31), except in December (χ^2=9.24, P<0.01 n=52).

Size and age at maturity

Weakfish mature at a small size and by age 1 in Chesapeake Bay. Most age 1 fish, and all age 2 fish were mature. Estimated mean length at first maturity (L_{50}) was 170 mm TL (S.E.=2.16) for females and 164 mm TL (S.E.=0.54) for males (Fig. 9). Histological examination confirmed fish this small actually spawn. Females as small as 174 mm TL had POFs, indicating recent spawning; and females as small as 199 mm TL had unovulated hydrated oocytes, indicating imminent spawning. Histological ovarian appearance of age 1 females > 170 mm TL was generally indistinguishable from that of older, larger fish.

Fig. 31. Monthly sex ratios for weakfish in the Chesapeake Bay region, 1990-1992. Hatched bars represent collections off North Carolina. Sample sizes are indicated above the bars and overall sex ratios for Chesapeake Bay are indicated below the year.

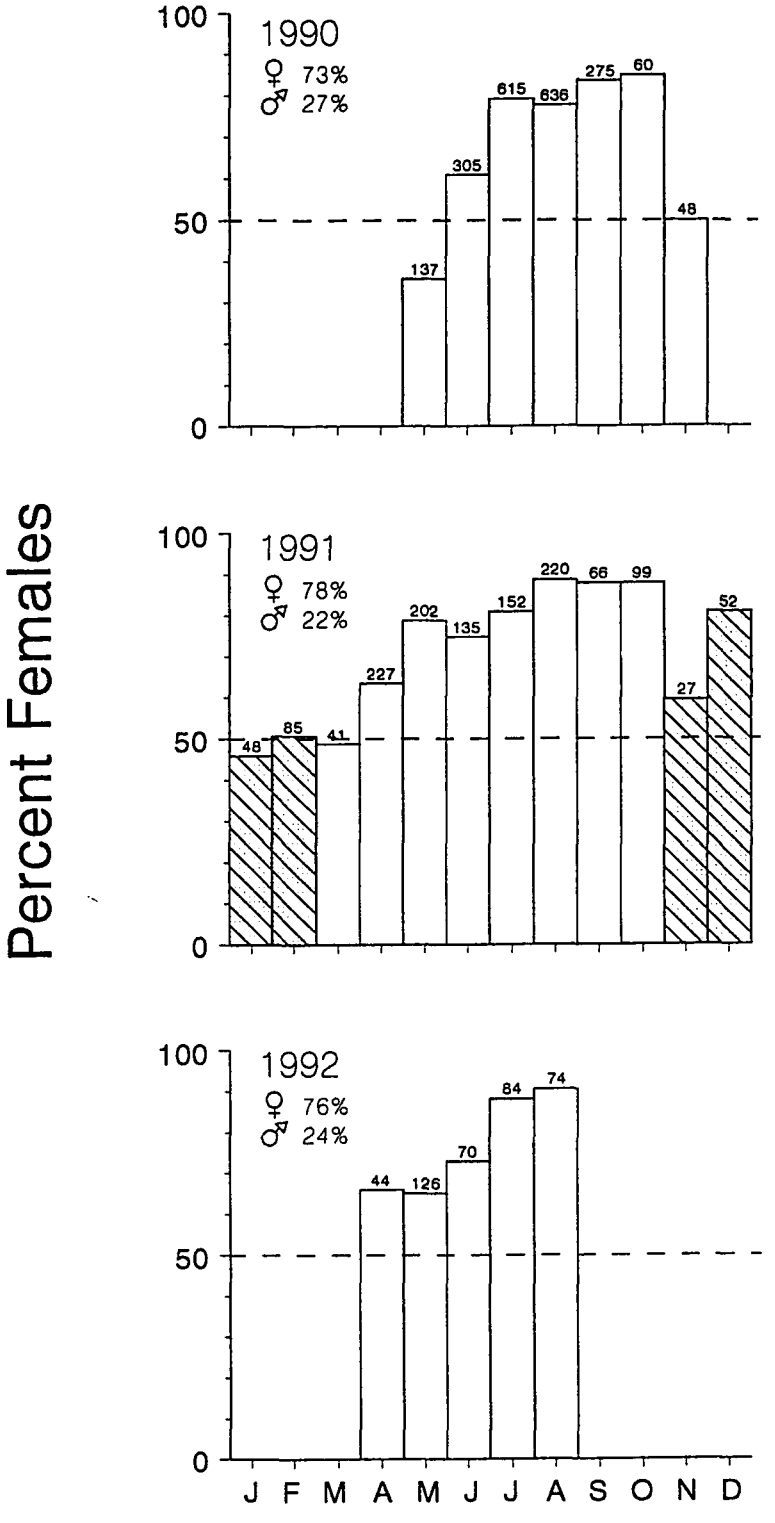

Percent Females
100
50
0
1990
♀ 73%
♂ 27%
137
305
615
636
275
60
48
1991
♀ 78%
♂ 22%
48
85
41
227
202
135
152
220
66
99
27
52
1992
♀ 76%
♂ 24%
44
126
70
84
74
J F M A M J J A S O N D
Month

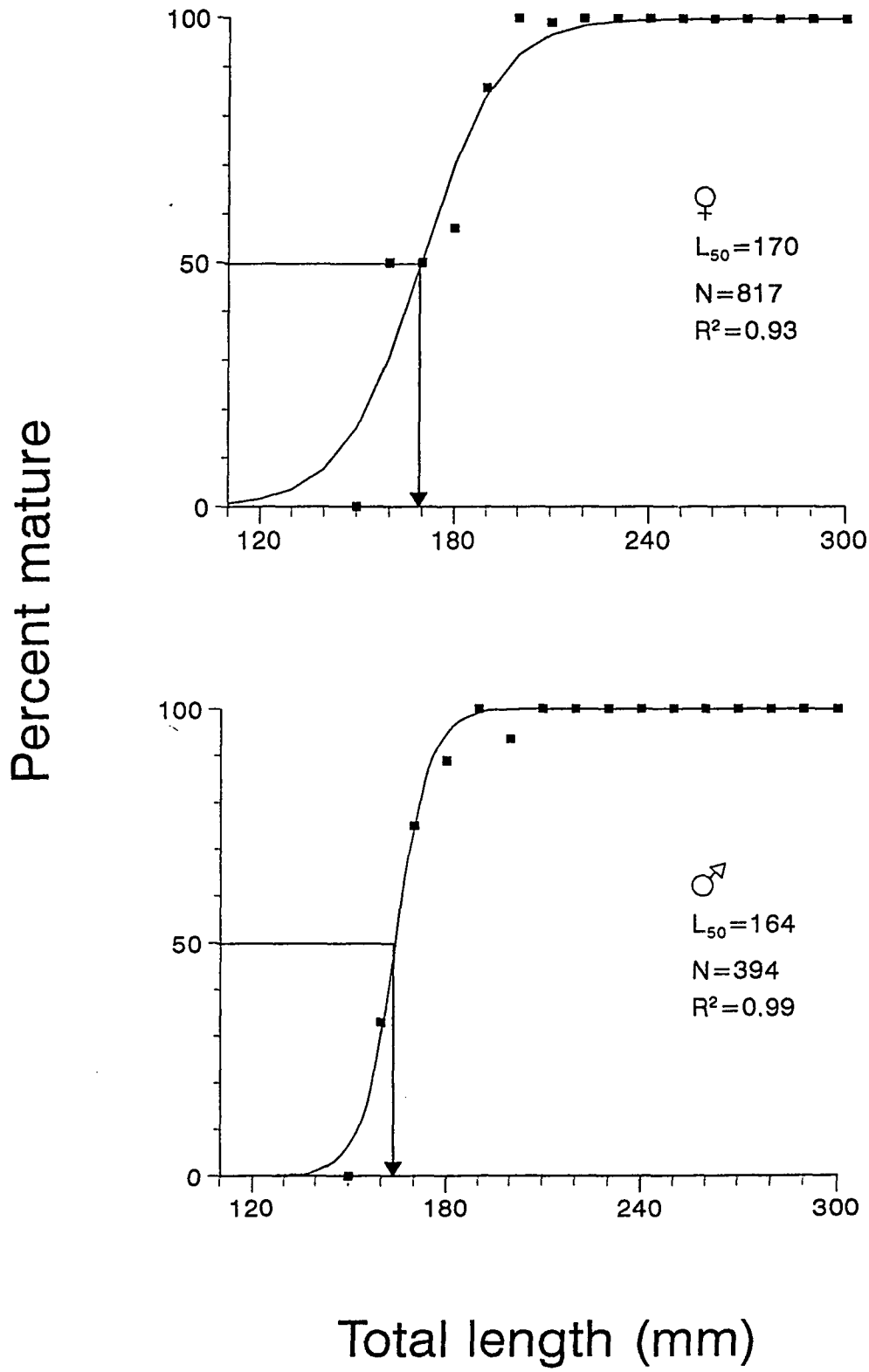
Table 12. Number of male and female weakfish by month and Chi-square tests of observed to expected (1:1) sex ratios, for the years 1990-1992. ** = P<0.01.

Year	Month	Males	Females	Chi-square
1990	May	88	49	5.51
	Jun	119	186	6.90 **
	Jul	128	487	103.45 **
	Aug	142	494	96.86 **
	Sep	45	230	60.67 **
	Oct	9	51	14.01 **
	Nov	24	24	0.01
1991	Mar	21	20	0.01
	Apr	83	144	7.63 **
	May	43	159	32.74 **
	Jun	34	101	15.53 **
	Jul	29	123	28.45 **
	Aug	25	195	64.91 **
	Sep	8	58	18.19 **
	Oct	12	87	26.65 **
1992	Apr	15	29	1.92
	May	44	82	5.43
	Jun	19	51	6.86 **
	Jul	10	74	23.63 **
	Aug	7	67	23.52 **

Table 13. Number of female and male weakfish collected in Chesapeake Bay by gear, and Chi-square tests of observed to expected (3:1) female to male sex ratios. α=0.01.

Year	Gear	Males	Females	% female	Chi-square
1990	haul seine	424	1,207	74	0.26
	gill net	66	188	74	0.03
1991	haul seine	58	229	80	0.85
	gill net	199	660	77	0.37
1992	haul seine	53	187	78	0.24
	gill net	41	120	75	0.00

Fig. 32. Percent mature female and male weakfish by 10 mm total length intervals, fitted to a logistic function. Arrows indicate mean length at first maturity (L_{50}). N=sample size.

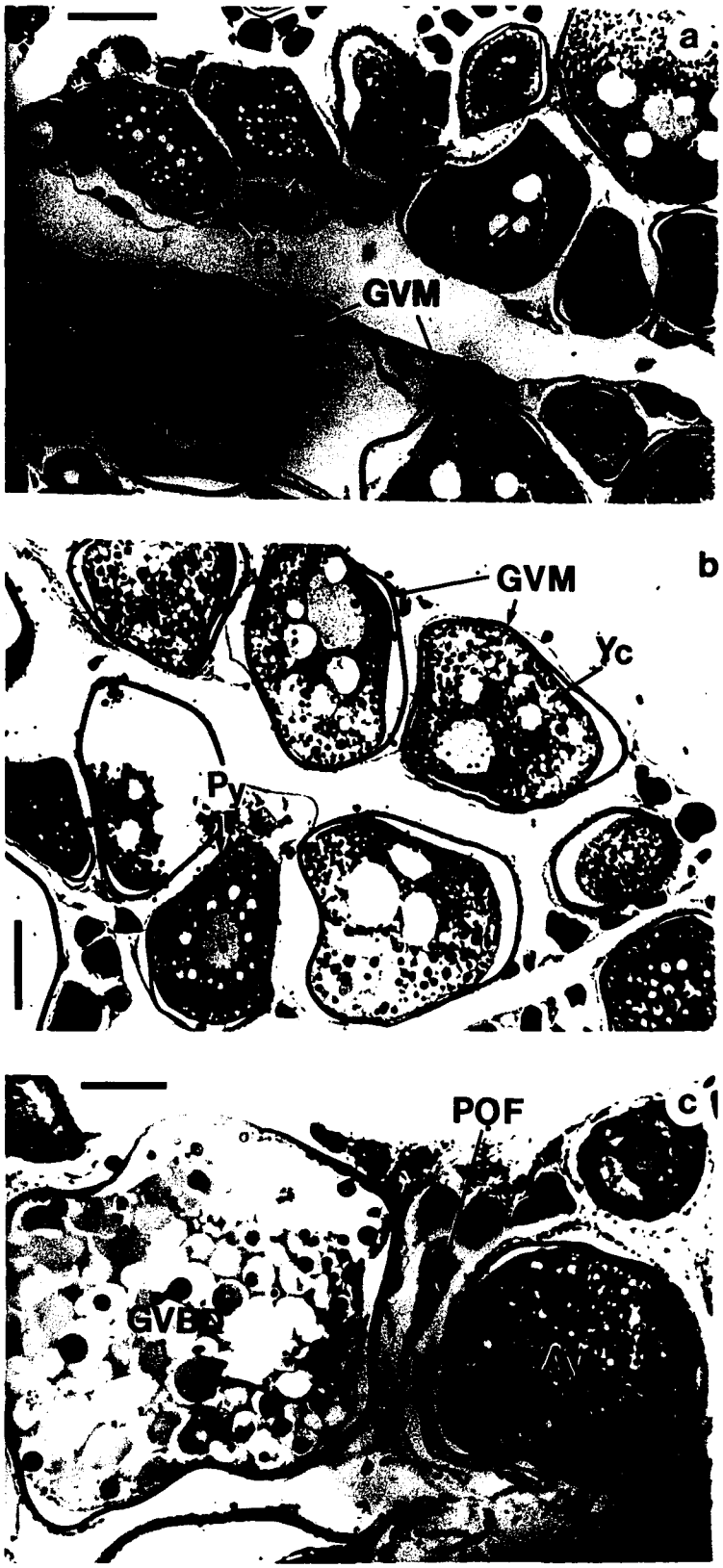

Percent mature
100
50
0
120
180
240
300
♀
L_{50}=170
N=817
R^2=0.93
100
50
0
120
180
240
300
♂
L_{50}=164
N=394
R^2=0.99
Total length (mm)

Diel Periodicity

Weakfish spawn primarily at dusk. Of the 34 gravid females collected with known kill-times, 32 were caught between 1700 and 2000 hrs. The remaining two females were collected between 0600 and 0900 hrs, suggesting individual variability in spawning time or the ability to retain hydrated oocytes if spawning conditions are not met. However, most females collected between 0600 and 0900 (17 out of 19) were partially spent.

Oocyte development the day a female will spawn also shows diel periodicity. At dawn (0600 hrs), females which will spawn that evening have late-stage advanced yolked oocytes which have begun lipid coalescence—i.e., many small oil vacuoles have begun to coalesce into several larger ones around the germinal vesicle. Between 0600 and 1000 germinal vesicle migration (GVM) begins (Fig. 33a), marking the initiation of FOM. The next-most-developed oocytes are partially-yolked. By 1400-1600 hrs, the germinal vesicle has migrated to the animal pole and yolk coalescence has begun (Fig. 33b). At this stage, whole oocytes begin to become translucent and are detectable macroscopically. Some of the next batch of yolked oocytes have gone from partially-yolked to early-stage advanced yolked. Between 1700 and 2000 hrs, gravid females can be in any stage from yolk plate (the last stage in yolk coalescence) to ovulation, although most have at least begun germinal

Fig. 33. Histological appearance of weakfish oocytes at different stages of final oocyte maturation (FOM): (a) 1000, beginning germinal vesicle migration (GVM), next most developed oocytes are partially-yolked (Py); (b) 1600, GVM has progressed and yolk coalescence (Yc) is beginning at the vegetal pole, next most developed oocytes are going from partially-yolked (Py) to early-stage advanced yolked; and (c) 1700, germinal vesicle breakdown (GVBD) has occurred and yolk coalescence has progressed throughout the oocyte. Next-most-developed oocytes are early-stage advanced yolked (Ay). Note 24-hr-old postovulatory follicle (POF) to the right of the GVBD oocyte. Bars=250 μm.


a
GVM
GVM
b
Yc
Py
POF
c
GVB

vesicle breakdown (Fig. 33c). The next-most-developed oocytes are in the early advanced yolked stage.

The diel periodicity of weakfish spawning is not equally evident, however, in samples from all commercial gears. Gill net catches contained fish killed throughout the day and night, with correspondingly varied stages of oocyte development. However, haul seines and pound net collections contained mainly fish killed at dawn, with partially-spent/redeveloping gonads. Consequently, most hydrated females (75%, N=134) were collected in gill nets even though this gear provided only 34% (N=2,884) of the females collected in Chesapeake Bay.

Ovulation and spawning in weakfish is quite rapid compared to final oocyte maturation. Of 747 females collected from a gill net fisherman in 1991, 80 were gravid and only 12 were running-ripe. The much lower incidence of running-ripe fish indicates the spawning process is more rapid than FOM/hydration. Oocyte development in known kill-time females supports this conclusion, as FOM began between 0600 and 1000 hours and was not completed until 1700-2000 hours. In contrast, the collection of two females at 2000 and 2100 hrs with fresh POFs and no hydrated oocytes suggests ovulation and spawning is completed within an hour or two of hydration.

Occasionally, females retained hydrated oocytes in the ovarian lumen for hours after ovulation. This was indicated

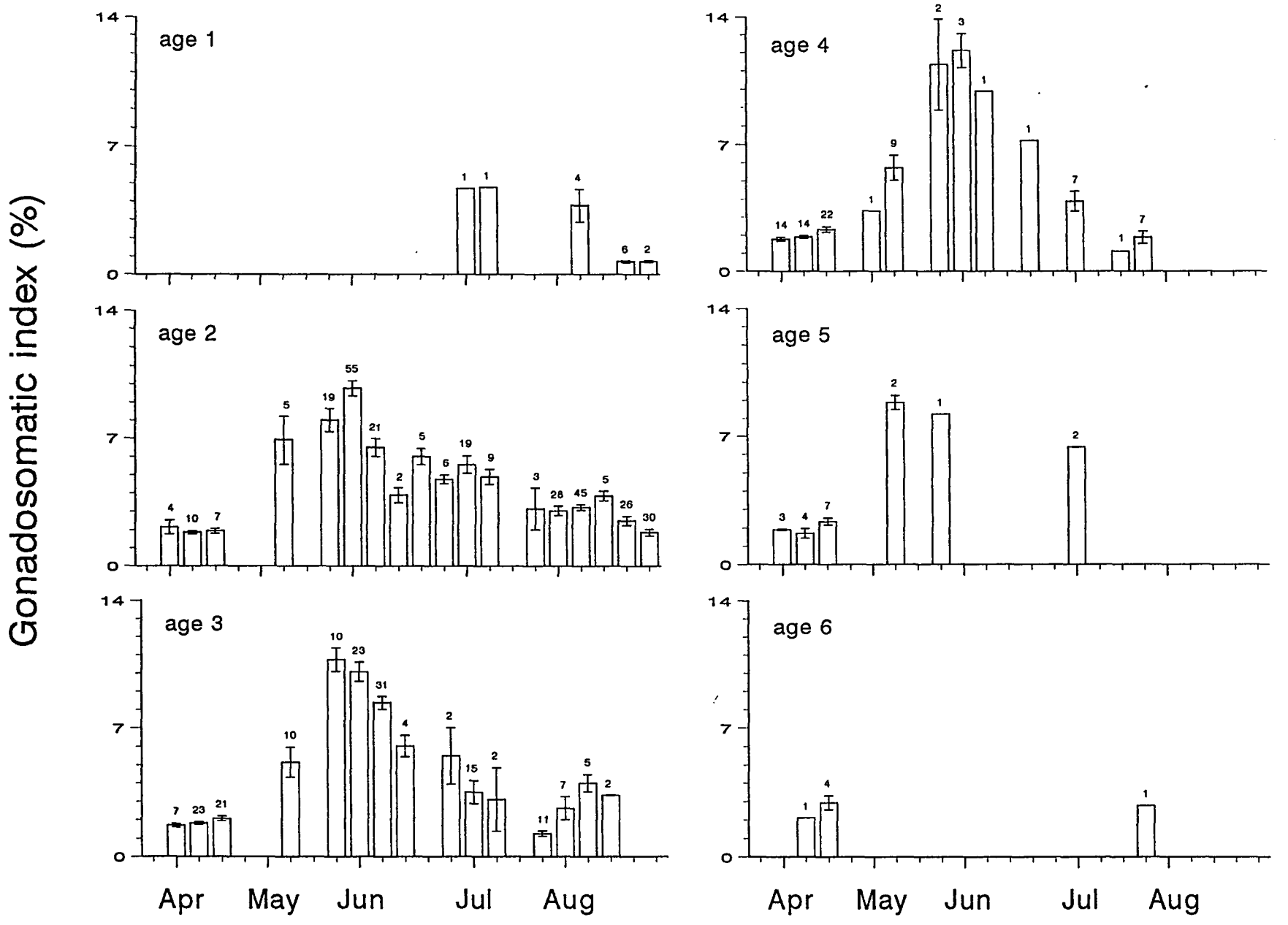
by a few ovaries which had either: (1) degenerating POFs and a large number of hydrated oocytes in the lumen; or (2) many hydrated oocytes but no POFs. It is unclear what caused the retention of these hydrated oocytes or how long they can remain viable in the ovary.

Age composition of spawning population

Older weakfish do not spawn over a longer time period than younger fish. Although one-year-olds had not yet entered the Bay in April, yolk deposition was apparent in all other ages (2-6), with no indication that older fish were more developed. Similarly, cessation of spawning showed no clear trend with age. Although most females > age 3 occurred in Chesapeake Bay in April and May before the spawning season began (Fig. 34), at least some age 1-5 females, which were about to spawn or had just recently spawned, occurred through mid-August. Mean weekly GSIs of nonhydrated females from Chesapeake Bay in 1991 (Fig. 34) indicated a similar pattern of ovarian development for all ages: GSIs peaked in late May/early June and remained above pre-spawning season GSI levels until at least July, and fish > age 3 did not show a more extended period of increased ovarian development than younger fish.

The age composition of female weakfish in Chesapeake Bay was dominated by 1 to 3-year-olds. Over the period 1990-1992, 82% of the female spawners were age 2 and 3

Fig. 34. Mean weekly gonadosomatic index ± one standard error for non-hydrated (not gravid or running-ripe) female weakfish in 1991, by age. Bold tick marks indicate the beginning of each month. Sample size is indicated above each bar.


Gonadosomatic index (%)
age 1
age 2
age 3
age 4
age 5
age 6
14
7
0
Apr
May
Jun
Jul
Aug

(Table 14). However, the relative contribution of spawners ages 1-3 fluctuated from year to year. Spawners consisted primarily of 1- and 2-year-olds in 1990, but ages 2-3 dominated in 1991 and 1992.

Age 1 fish were less abundant in the spawning population than in the general population. The percentage of age 1 spawners was consistently lower than the percentage of age 1 females in yearly samples (Table 14). Mean lengths of age 1 females in May and June were 176 mm TL (N=42) and 200 mm TL (N=41), respectively, with many females occurring which were smaller than the L_{50} value of 170 mm TL. Thus, smaller females may not join the spawning population until part-way through the spawning season.

Spawning activity

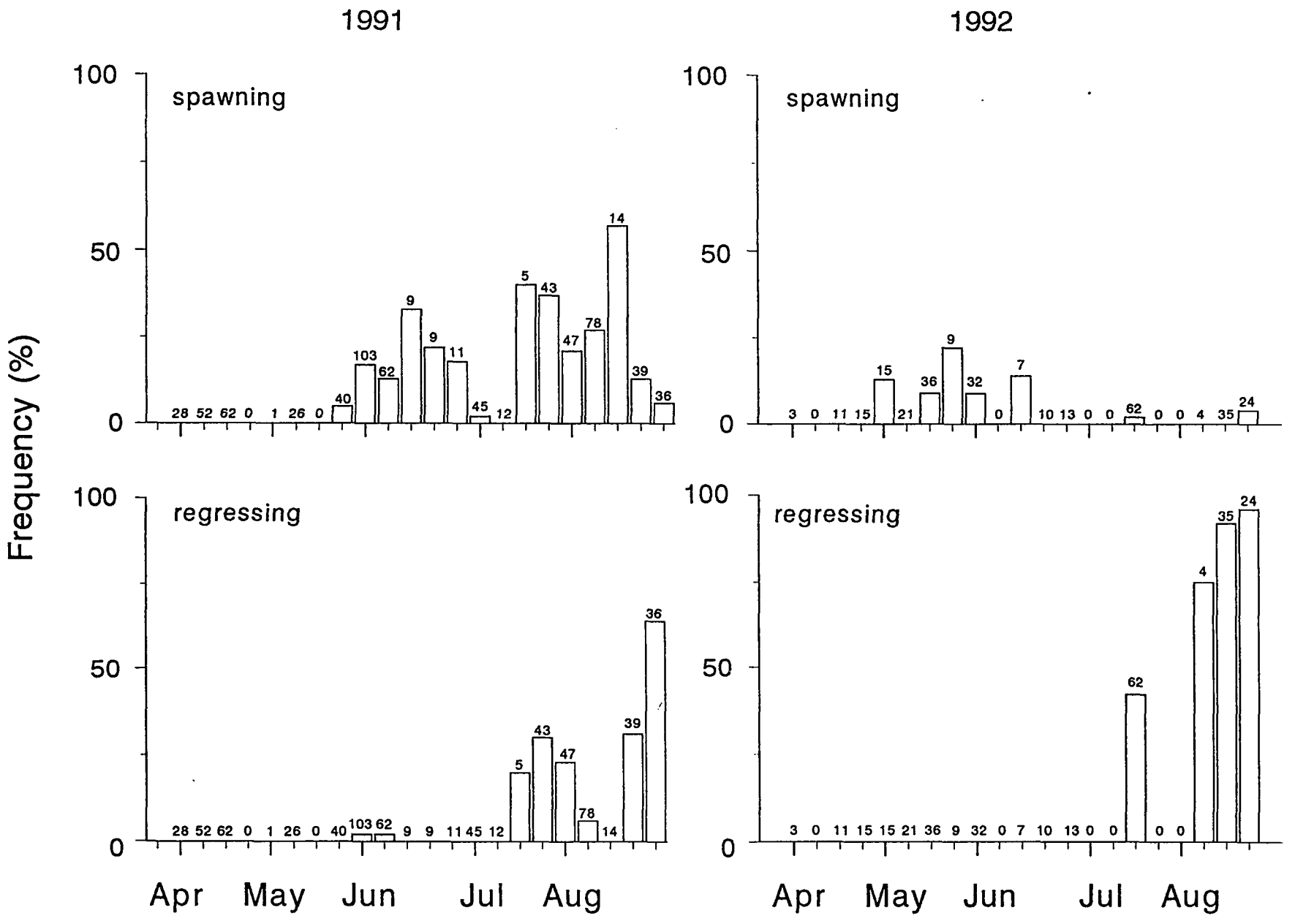
Most gravid females were collected by gill nets in 5-6 m of water. Gill nets were set on a muddy bottom, approximately 0.2 Km from shore, inshore from a 9-12 m deep channel. Most gravid females were caught moving in toward shore, where the bottom becomes sandy and the water is less than 4 m deep.

Although spawning females were collected from May through August in 1991 and 1992, spawning activity was not evenly spaced over this time period. In 1991, spawning (gravid and running-ripe) females were common from mid-May through June (Fig. 35). Their abundance decreased

Table 14. Age composition (%) of all female weakfish and of spawners (gravid, running-ripe, or with POFs) collected in Chesapeake Bay during the spawning season, by year, and pooled over years, 1990-1992.

Year	Age	# all females	Age comp. all females	# spawners	Age comp. spawners
1990	1	169	51.52	4	23.53
	2	120	36.59	9	52.94
	3	15	4.57	1	5.88
	4	11	3.35	1	5.88
	5	5	1.52	2	11.76
1991	1	23	4.13	4	3.03
	2	352	63.20	96	72.73
	3	143	25.67	27	20.45
	4	32	5.75	4	3.03
	5	6	1.08	1	0.76
	6	1	0.18	0	0.00
1992	1	31	11.70	1	2.56
	2	128	48.30	11	28.21
	3	88	33.21	23	58.97
	4	14	5.28	2	5.13
	5	3	1.13	1	2.56
	6	1	0.38	1	2.56
Pooled	1	223	19.39	9	4.79
	2	600	52.17	116	61.70
	3	246	21.39	51	20.13
	4	57	4.96	7	3.72
	5	14	1.22	4	2.13
	6	2	0.17	1	0.53

Fig. 35. Weekly frequency of spawning and regressing female weakfish in Chesapeake Bay in 1991/1992. Spawning= gravid+running-ripe females; regressing=regressing+ resting females. Weekly female sample size is indicated above each bar. Bold tick marks indicate the beginning of each month.


1991
1992
spawning
regressing
Frequency (%)
100
50
0
28 52 62 0 1 26 0 40 103 62 9 9 11 45 12 5 43 47 78 14 39 36
3 0 11 15 21 36 9 32 0 7 10 13 0 0 62 0 0 4 35 24
3 0 11 15 15 21 36 9 32 0 7 10 13 0 0 62 0 0 4 35 24
Apr
May
Jun
Jul
Aug

in July—with only 3 out of 62 females collected in the first three weeks of July being gravid or running-ripe. During this same time period, weakfish ovaries showed thickened ovarian membranes, few yolked oocytes, increased oocyte atresia and vascularization—indicating cessation of spawning—and a large percentage of regressing females occurred for the first time in the last week of July (Fig. 35). However, a large percentage of spawning females also reoccurred by the last week of July and both spawning and regressing females continued to be present throughout August. In 1992, a decreased number of spawning females again occurred in July along with the first occurrence of regressing females. In contrast to 1991, the percentage of spawning females in August 1992 did not return to the levels seen earlier in the season and most females in August 1992 had regressing ovaries, indicating they had ceased spawning.

There was no clear relationship between the daily percentage of spawning females which occurred in 1991 and the lunar cycle. Although large percentages of spawning females sometimes occurred near the full moon (Fig. 36, Table 15), they also occurred at other times, and showed no monthly or fortnightly peaks, as would be expected if there was a correlation between spawning and any one lunar phase.

Water temperature does not appear to have limited spawning activity in 1991 and 1992. Mean weekly water temperatures at the mouth of the York River ranged from

Fig. 36. Percent hydrated (gravid and running-ripe) female weakfish in daily gill net collections during 1991, beginning on May 22. Squares represent days fish were not collected. Blank spaces indicate when < 2 females were caught. F's indicate a full moon. N=sample size.

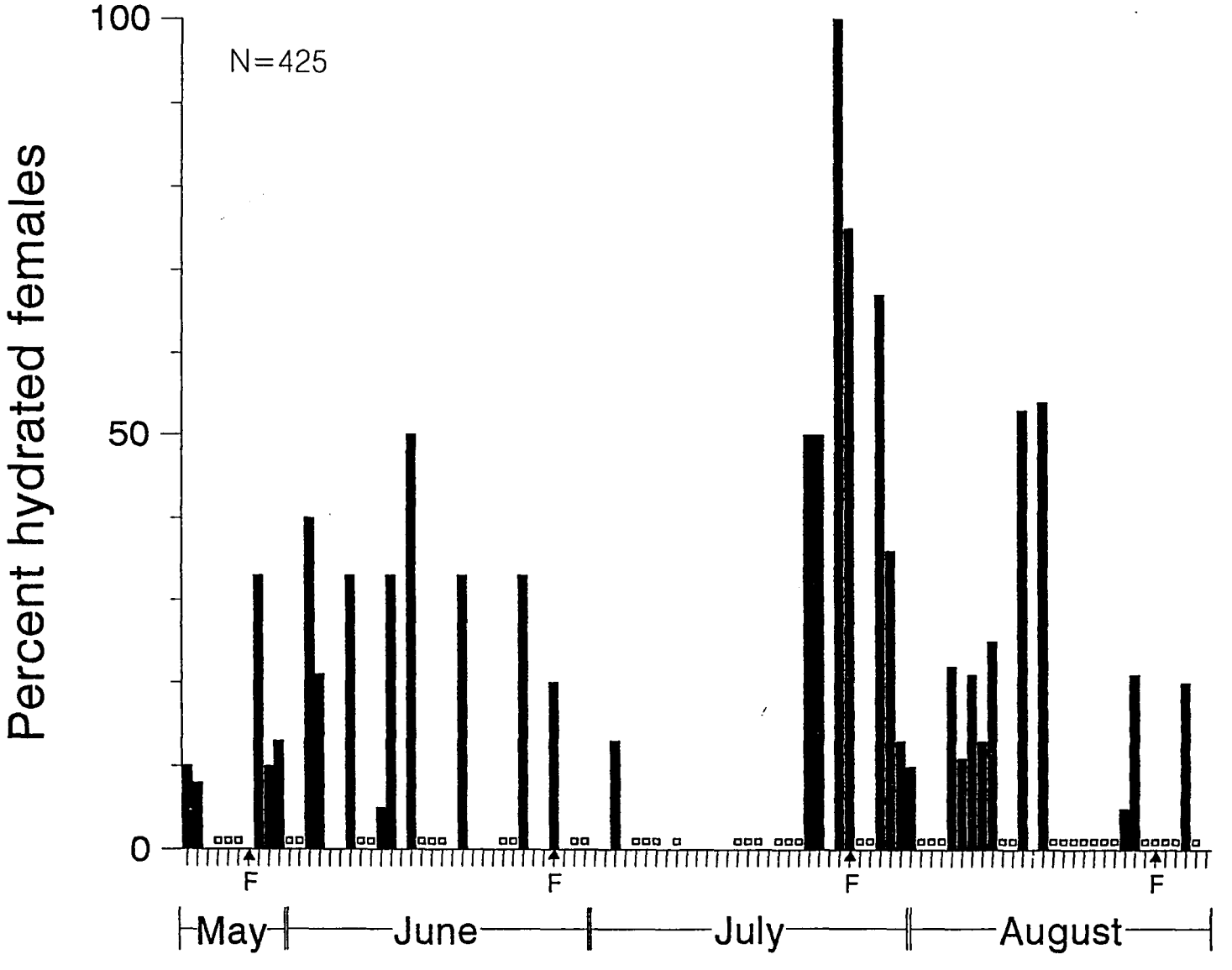

100
50
0
N=425
Percent hydrated females
F
F
F
F
May
June
July
August

Table 15. Total number females and number hydrated (gravid or running-ripe) in 1991 daily gill net catches. *'s indicate when full moons occurred.

Date	Number females	Number hydrated	Date	Number females	Number hydrated
5/22	10	1	7/4	2	0
5/23	13	1	7/8	8	0
5/24	12	0	7/10	5	0
5/28*	6	0	7/11	7	0
5/29	3	1	7/12	0	0
5/30	10	1	7/13	0	0
5/31	8	1	7/14	0	0
6/3	10	4	7/18	0	0
6/4	19	4	7/22	4	2
6/5	10	0	7/23	8	4
6/6	3	0	7/24	0	0
6/7	9	3	7/25	0	0
6/10	21	1	7/26*	4	3
6/11	3	1	7/29	9	6
6/12	0	0	7/30	11	4
6/13	4	2	7/31	8	1
6/17	2	0	8/1	10	1
6/18	3	1	8/5	18	4
6/19	2	0	8/6	9	1
6/20	2	0	8/7	19	4
6/21	0	0	8/8	15	2
6/24	3	1	8/9	16	4
6/25	3	0	8/12	19	10
6/26	1	1	8/13	1	1
6/27*	5	1	8/14	13	7
6/28	2	0	8/22	20	1
7/1	6	0	8/23	19	4
7/2	1	0	8/25*	-	-
7/3	8	1	8/28	4	2

18.3-28.6^0 C (Fig. 37) during the 1991 and 1992 spawning seasons. In 1991, water temperatures peaked in the last three weeks in July, with mean weekly temperatures above 28^0 C. However, a large percentage of spawning females occurred in the last week of July 1991. In July 1992, mean weekly water temperatures were considerably lower (24.7^0-26.5^0), and water temperature did not peak until the first week of August, at 27.5^0 C. Thus, the decreased spawning activity seen in both 1991 and 1992 in early July was not due to an upper temperature threshold. Water temperatures also do not explain the different pattern of spawning activity in 1991 versus 1992, as late July-August 1992 temperatures were within the range at which weakfish spawned in 1991.

Food availability and body condition, however, showed temporal patterns similar to those seen in spawning activity. Food availability in late July-August was greater in 1991 than in 1992, as evidenced by the higher percentage of "full" fish (Fig. 38). Spawning females were also more prevalent in July-August in 1991 than in 1992 (Fig. 35). Mean condition of age 2 and 3 fish in April-August differed significantly by month in both 1991 (ANOVA, N=697, F=30.51, P=0.0001) and 1992 (ANOVA, N=284, F=35.52, P=0.0001). In 1991, condition was highest in April and May (Fig. 39) corresponding to the time at which females had fully-developed ovaries, but before most spawning began. Condition was at its lowest in June (age 2) and July (age 3) and few spawning females occurred in the first three weeks

Fig. 37. Mean weekly water temperature at the mouth of the York River for 1991/1992. Dashed lines demarcate when weakfish spawn in Chesapeake Bay.

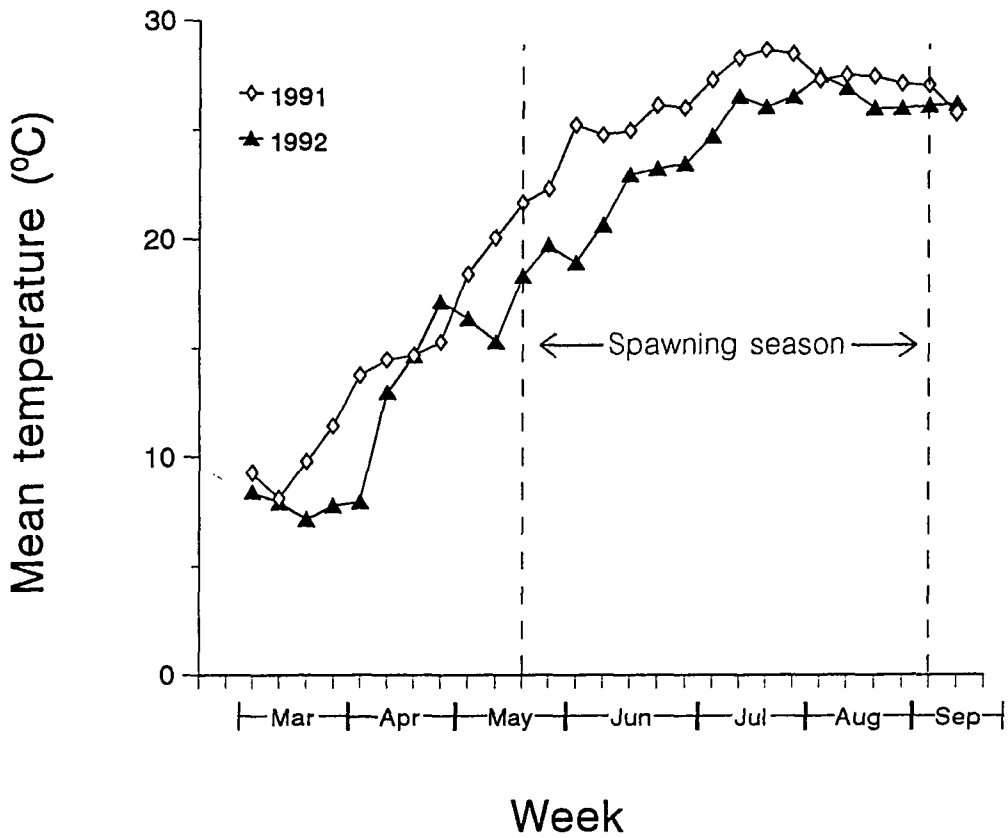
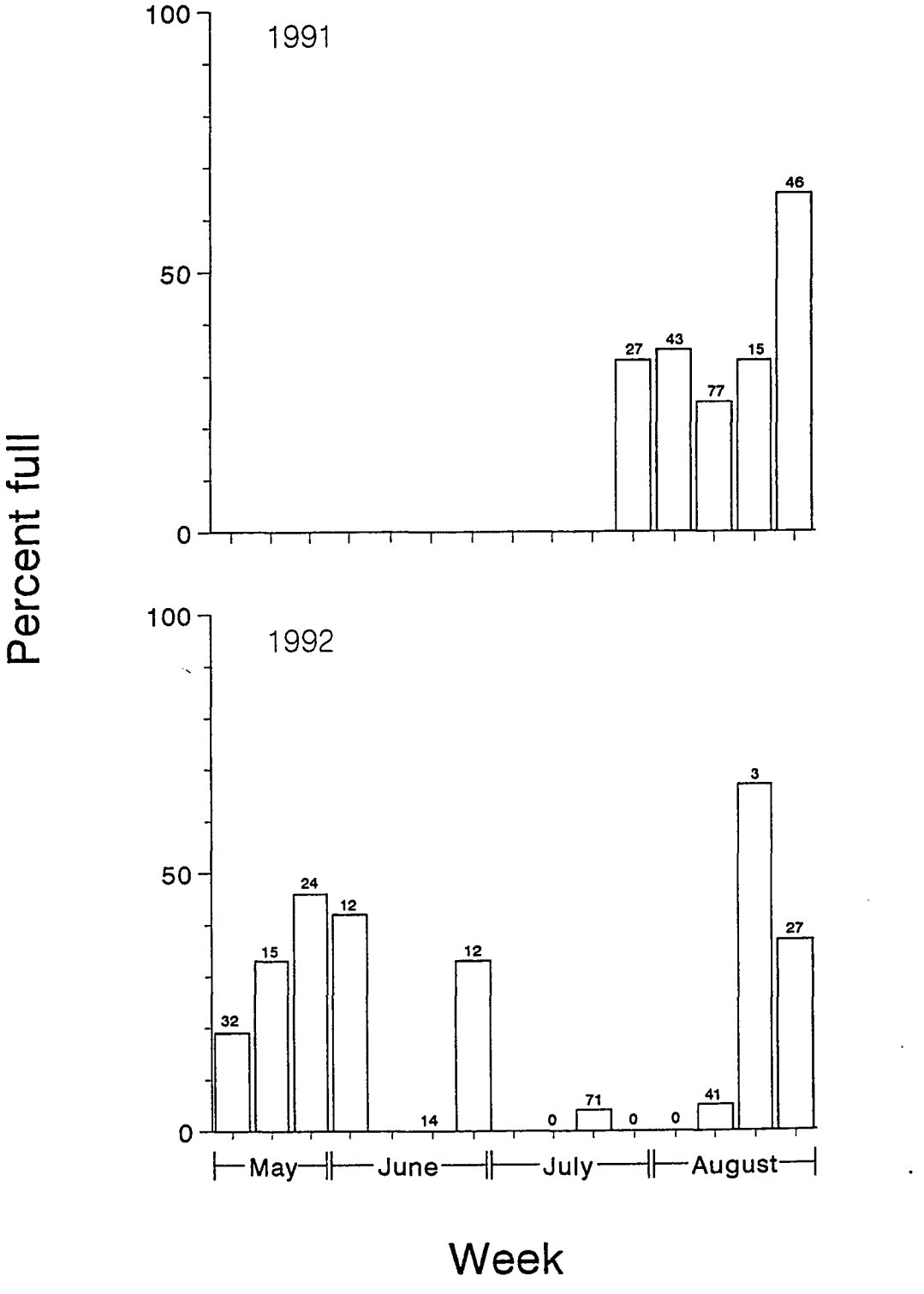

30
20
10
0
Mean temperature (°C)
1991
1992
Spawning season
Mar
Apr
May
Jun
Jul
Aug
Sep
Week

Fig. 38. Mean weekly percent of weakfish in Chesapeake Bay designated as full in 1991/1992. Sample sizes are indicated above each bar. Zeros represent weeks when no fish were caught.


Percent full
100
50
0
1991
27
43
77
15
46
1992
32
15
24
12
14
12
0
71
0
0
41
3
27
May
June
July
August
Week

of July. Condition recovered in the second half of the spawning season for both age groups, coinciding with the reoccurrence of large numbers of spawning females.

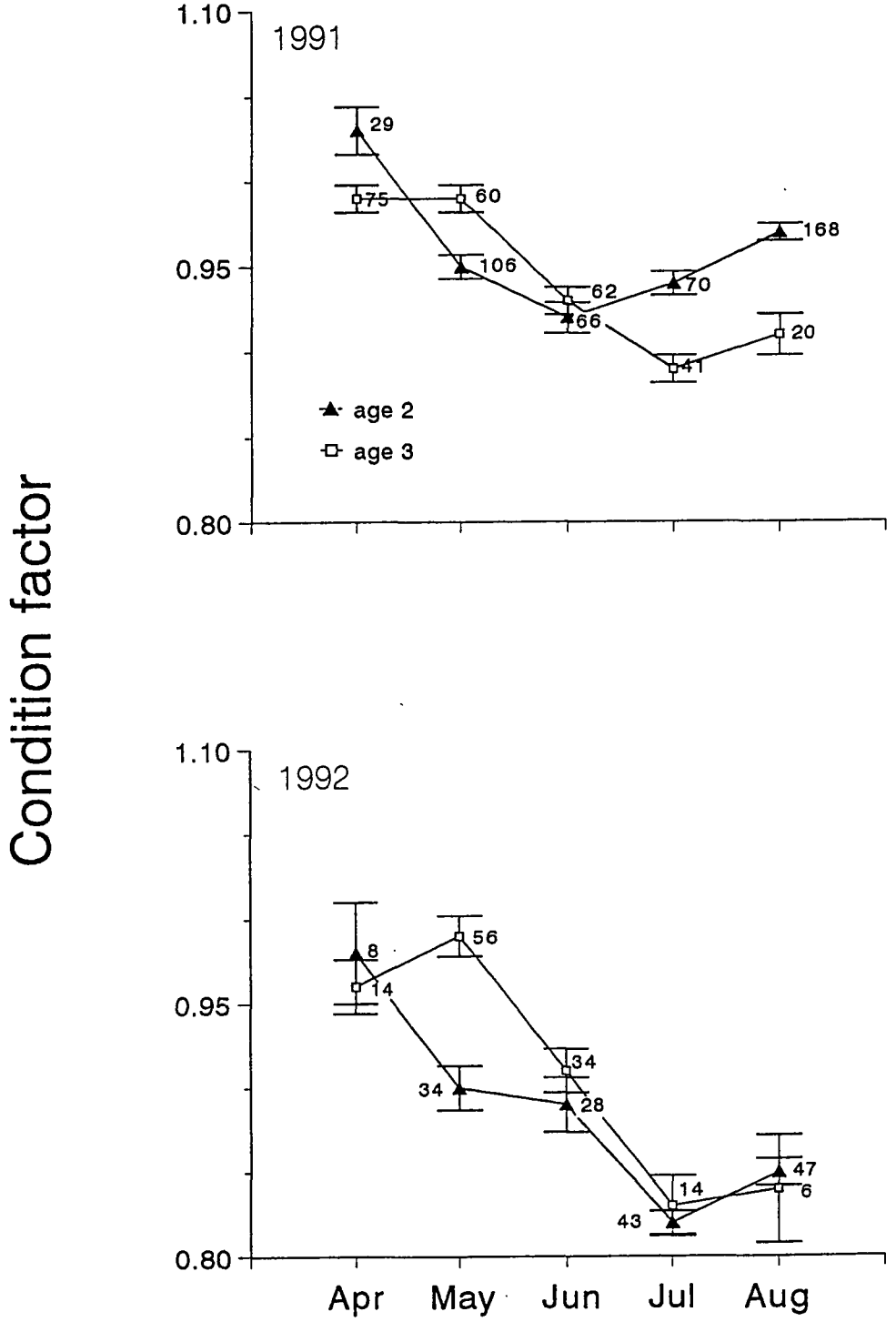
In 1992, monthly condition showed a significantly different pattern than that of 1991 (ANOVA, N=981, F=106.35, P=0.0001). In 1992, condition decreased steeply, reaching a significantly lower level in July than in 1991 (ANOVA, N=168, F=94.76, P=0.0001), and although a slight recovery occurred in August, condition remained significantly lower than in 1991 (ANOVA, N=241, F=136.26, P=0.0001). Coinciding with the lower 1992 condition in July and August, few spawning females were collected during this time period, in contrast to the pattern seen in 1991.

Batch fecundity

Hydrated oocytes in gravid ovaries were evenly distributed. Differences in hydrated oocyte counts were not significant between posterior, middle and anterior sections of the right ovary (N=50, F=0.01, P=1.00). There was also no significant difference between right and left ovaries (N=50, F=0.00, P=0.98).

Although there was much individual variation in batch fecundity, there were significant relationships between batch fecundity and fish size. Batch fecundity-at-size fell within a similar range for fish collected in 1991 and 1992 and showed no clear relationship with month of collection

Fig. 39. Mean monthly Fulton's condition factor ± one standard error for age 2 and 3 weakfish in 1991/1992. Sample sizes are indicated.


1.10
1991
0.95
0.80
29
75
60
106
62
66
70
41
168
20
age 2
age 3
1.10
1992
0.95
0.80
8
14
56
34
34
28
14
43
47
6
Apr
May
Jun
Jul
Aug
Condition factor
Month

(Fig. 40). Batch fecundities (BF) in 1991 and 1992, ranged from 75,289 to 517,845 eggs/female, and BF significantly increased with TL (ANOVA, N=62, F=66.52, P=0.0001) in the following manner:

$$BF = -349{,}558 + 1{,}544\ TL\ (R^2=0.53,\ N=62)$$

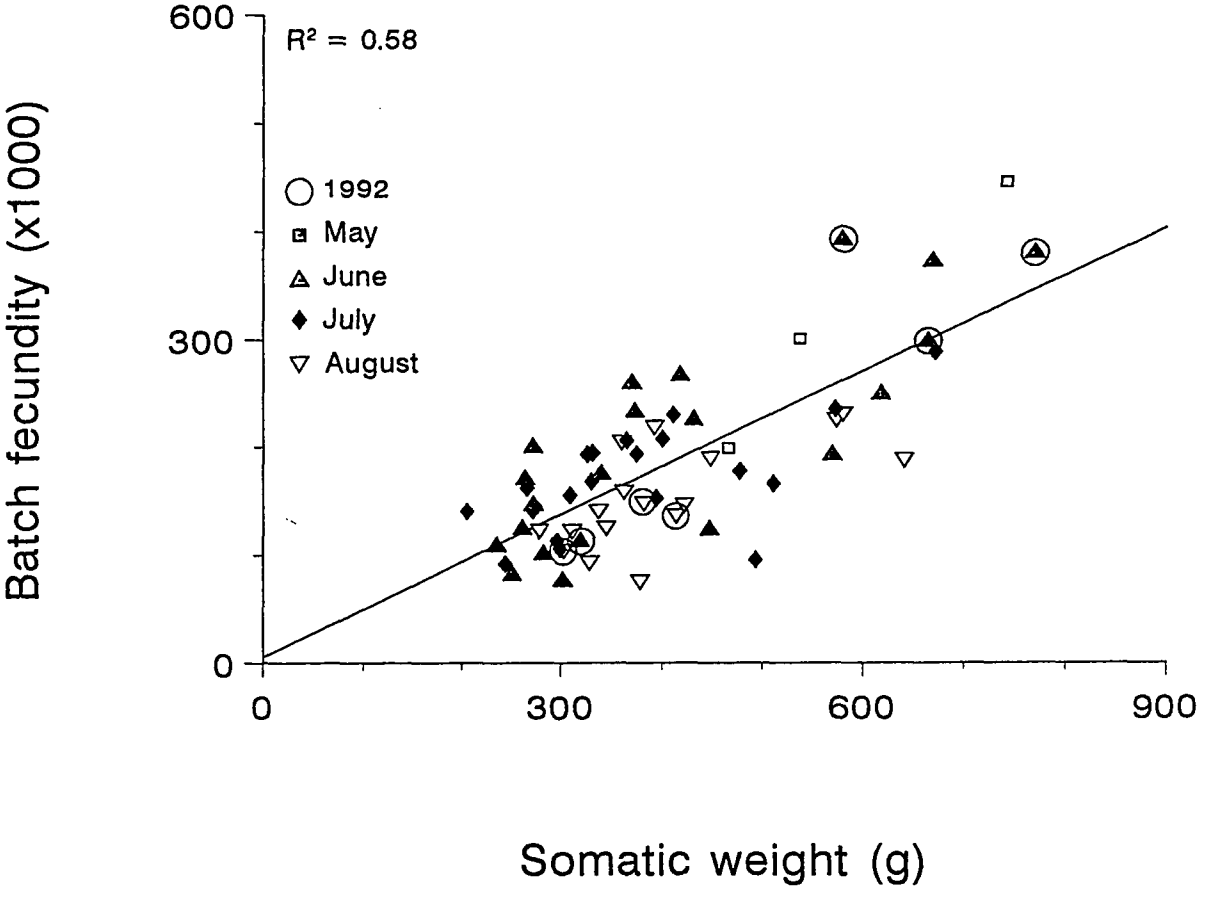
The BF to somatic weight (SW) relationship was also significant (ANOVA, N=62, F=84.23, P=0.0001) and showed a somewhat better fit (Fig. 40). The equation was:

$$BF = 7{,}244 + 439.7\ SW\ (R^2=0.58,\ N=62).$$

As expected from the BF-at-size relationships, BF increased with age. BF of one age 1 fish was 121,972 eggs, while mean BF at age 2 was 153,099 eggs (N=39), and at age 3 was 295,403 eggs (N=12). BF of one age 4 female collected in Delaware Bay, was 653,790 eggs. Also, due to the relationship between BF and fish size, mean BF was greater in 1992 (226,007 eggs) than in 1991 (179,750 eggs), as 1992 gravid females were slightly larger than those in 1991.

Relative fecundity did not have a significant relationship with TL (ANOVA, N=62, F=0.383, P=0.5381) or SW (ANOVA, N=62, F=0.235, P=0.6296), indicating larger fish do not produce more eggs per gram SW. Similarly, eggs/gram

Fig. 40. Regression of batch fecundity on somatic weight of weakfish, pooled for 1991/1992. Fish collected in 1992 are marked by a circle around the symbol, all others were collected in 1991.


600
300
0
R^2 = 0.58
1992
May
June
July
August
Batch fecundity (x1000)
0
300
600
900
Somatic weight (g)

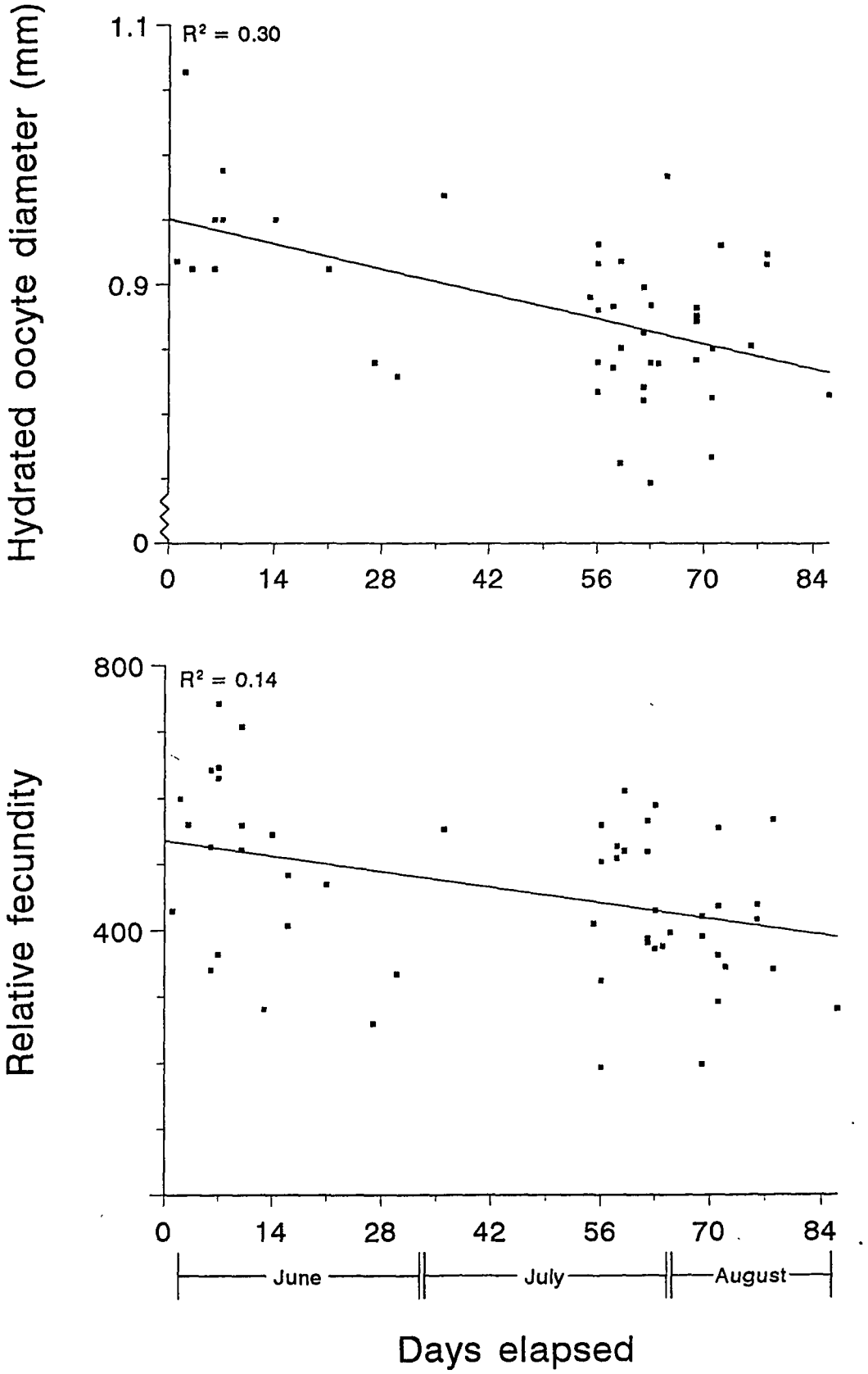
ovary did not have a significant relationship with TL (ANOVA, N=62, F=1.479, P=0.2287) nor with SW (ANOVA, N=62, F=1.374, P=0.2457).

In 1991, relative fecundity and hydrated oocyte diameter decreased as the spawning season progressed (Fig. 41). Mean hydrated oocyte diameter ranged from 0.75-0.98 mm and significantly decreased over the 1991 spawning season (ANOVA, N=45, F=18.32, P=0.0001). Relative fecundity also decreased significantly as the spawning season progressed (ANOVA, N=55, F=8.45, P=0.0005).

Spawning frequency

Spawning frequency in Chesapeake Bay was much higher in 1991 than in 1992. In 1991, 62% of the females caught at dusk over the spawning season were gravid or running-ripe, corresponding to a spawning frequency of once every 1.6 days. In comparison, a spawning frequency of once every 2.6 days was estimated by the POF method. In 1992, however, only 8.5% of the females caught at dusk were gravid or running-ripe, corresponding to a spawning frequency of once every 11.7 days. A spawning frequency of every 12.6 days was estimated by the POF method. The occurrence of some females with both degenerating POFs and FOM oocytes in their ovaries (Fig. 34c)—signifying daily spawning—indicates weakfish are capable of spawning at the high frequencies estimated for 1991.

Fig. 41. Regression of mean hydrated oocyte diameter/ovary (N=20) and relative fecundity (batch fecundity/ somatic weight) of weakfish on days elapsed since May 28, 1991.


Hydrated oocyte diameter (mm)
1.1
0.9
0
R² = 0.30
0
14
28
42
56
70
84
Relative fecundity
800
400
R² = 0.14
June
July
August
Days elapsed

Annual fecundity

There was no evidence of asynchronous groups of spawners in the Chesapeake Bay. Thus, a general spawning season of May 15-August 28 (106 days) was used to estimate annual fecundity. No developing weakfish were collected after May (Fig. 26), indicating groups of lesser-developed females did not enter the Bay after spawning was initiated. In addition, gravid ovaries appeared more vascularized and flaccid later in the spawning season (Fig. 26c), and relative fecundity and hydrated oocyte diameter declined over the 1991 season—the expected pattern if one group of fish is spawning throughout the spawning season, increasingly using up their energy stores. Further evidence of one spawning group is the similarity of mean TLs of gravid females collected in May and June (349 mm TL, N=20, SE=9.2) with mean TLs of gravid females collected in July and August (341 mm TL, N=35, SE=5.6), and the predominance of age 2 and 3 spawners throughout the 1991 spawning season.

Annual fecundity estimates were 4-6x higher in 1991 than in 1992. Although mean BF was larger in 1992 than in 1991, the 1992 spawning frequency was considerably less (Table 16). The estimated 1991 spawning frequency of once every 1.6-2.6 days, corresponded to 41-66 spawns/female over the 106 day spawning season (Table 16). In comparison, the 1992 spawning frequency estimates of once every 11.7-12.6 days, corresponded to 8-9 spawns/female over the spawning

season (Table 16). Consequently, 1992 annual fecundity estimates were 1.8-2.0 million eggs/female, considerably less than the 1991 estimates of 7.4-11.9 million eggs/female.

Atresia

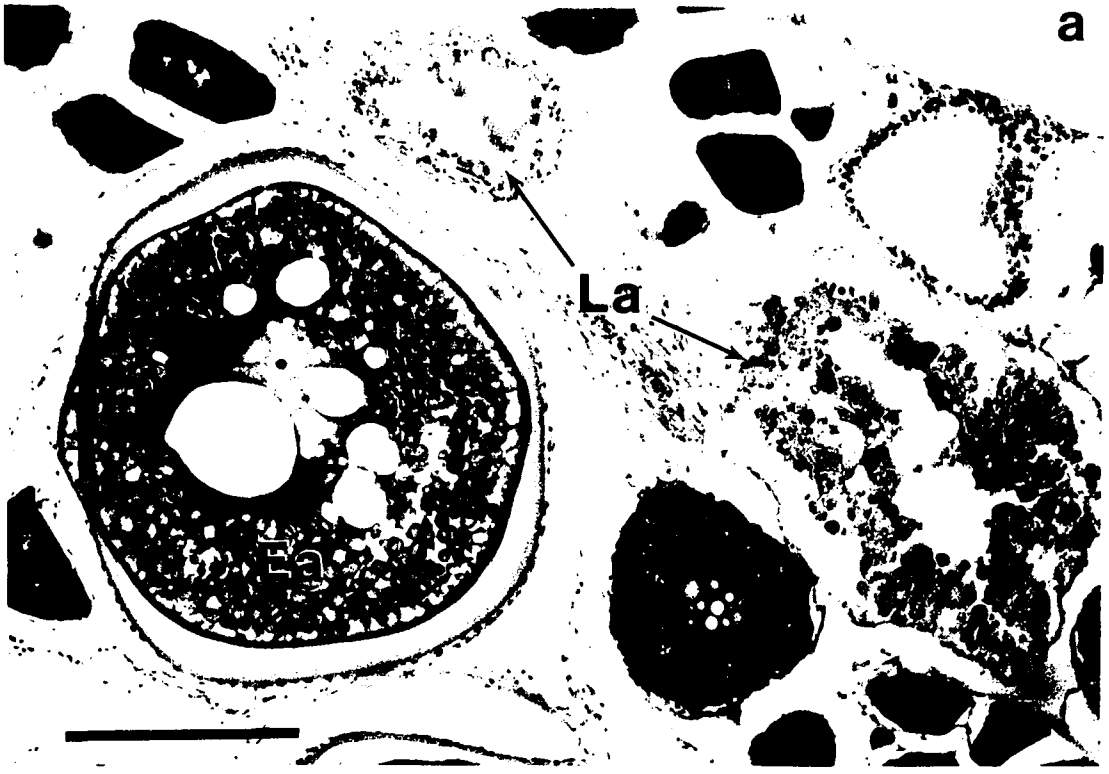
Atretic oocytes occurred in weakfish ovaries throughout the spawning season in 1991 and 1992. Early-stage α atresia of advanced yolked oocytes was indicated by: (1) homogeneous, basophilic staining around the nucleus; (2) an increase in vacuoles, sometimes several large slightly irregular-shaped vacuoles and other times a proliferation of small, round vacuoles; (3) yolk vesicles losing their integrity, as indicated by their irregular shape; and (4) a break-down of the zona radiata as it takes on a "scalloped" appearance, becoming uneven in diameter and losing its striations (Fig. 42a). Atretic advanced yolked oocytes also sometimes had a band of basophilic material around the periphery of the cytoplasm. This basophilic material occasionally leached out of the oocyte and accumulated between the zona radiata and the inside of the follicle.

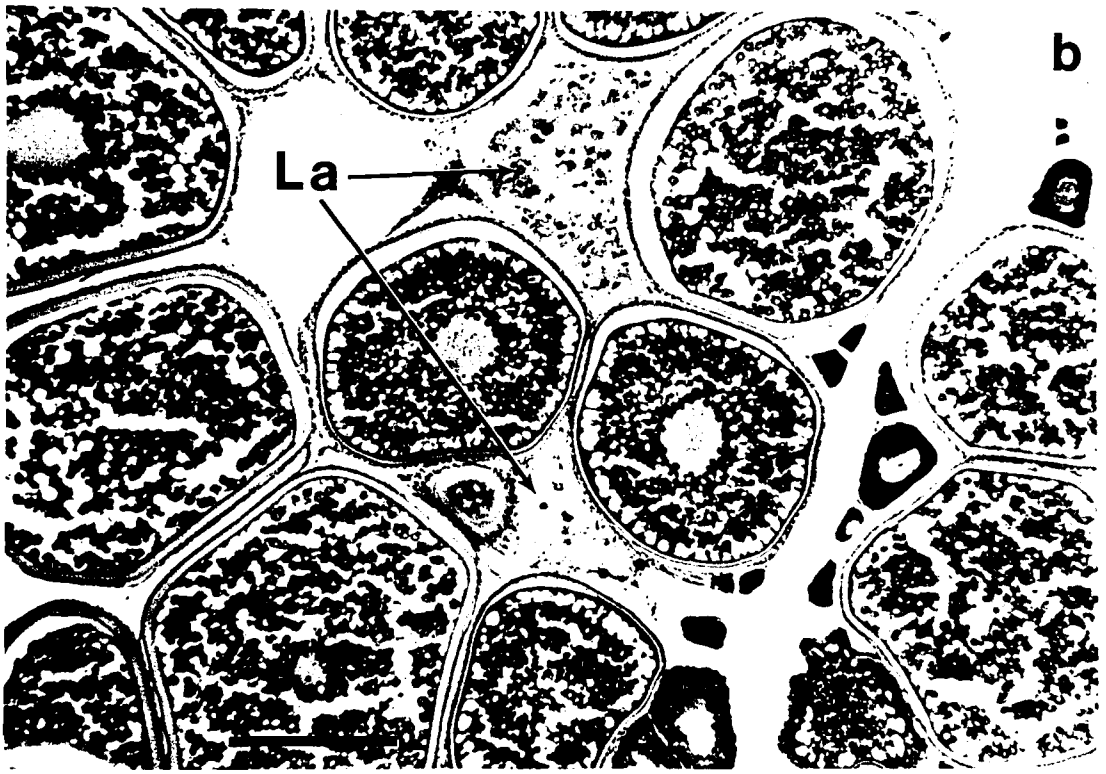
In late-stage α atresia, the zona radiata became discontinuous, breaking into sections. Phagocytizing granulosa cells invaded the oocyte and yolk vesicles continued to disintegrate, in places becoming an amorphous, eosinophilic mass surrounded by less-dissolved yolk vesicles

Table 16. Parameter estimates used to calculate mean annual fecundity/female, 1991-1992. POF=postovulatory follicle method. Hyd=hydrated oocyte method.

		1991	1992
Age composition (%) (5/15-8/28)	age 2	66	53
	3	29	34
	4	4	10
	>4	1	3
Mean TL (mm) of gravid females:		344	364
Mean batch fecundity:		179,750	226,007
Spawning frequency			
	(POF):	1 spawn/2.6 days	1 spawn/12.6 days
	(Hyd):	1 spawn/1.6 days	1 spawn/11.7 days
Spawns per female	(POF):	41	8
	(Hyd):	66	9
Mean annual fecundity	(POF):	7,369,750	1,808,056
	(Hyd):	11,863,500	2,034,063

Fig. 42. Histological appearance of: (a) a resorbing ovary from 7/8/91 with GSI=2.8 and early-stage α atresia of advanced yolked oocytes (Ea) and later-stage α atresia (La)—as indicated by the breakdown of the zona radiata (right) as well as late-stage α atresia going to β-stage (upper left); and (b) a healthy ovary from 6/2/92 with GSI=11.3, and a large number of advanced yolked oocytes going through late-stage α atresia (La). Bars=250 μm.


a
La
Ea


b
La

(Fig. 42a).

β stage atresia, the first stage of follicular atresia, began after all yolk vesicles and cytoplasm were resorbed. The transition from α to β stage atresia is characterized by an amoeboid-shaped, basophilic structure made up of invading granulosa cells surrounded by thecal cells, vacuoles and a few remaining yolk vesicles (Fig. 42a). After all the yolk has been resorbed, the structure collapses and becomes much smaller, looking similar to a degenerating POF.

Different patterns of atresia were present in weakfish ovaries, depending on when they were collected in the spawning season. Early in the season, some ovaries had a large number of α stage atretic yolked oocytes, occasionally a whole batch, surrounded by healthy advanced yolked oocytes (Fig. 42b). Large numbers of advanced yolked oocytes with α and β stage atresia were also sometimes present in gravid ovaries. However, the presence of many healthy oocytes along with atretic oocytes indicated this type of atresia did not signify complete resorption, as seen at the end of the spawning season. Rather, it may be due to different hormonal signals for initiation of yolk deposition versus FOM, i.e., if a batch of advanced yolked oocytes develops but the hormonal signal for FOM does not occur within a certain time frame, they will be resorbed and another batch of yolked oocytes will develop to take their place. Such a "conveyor belt" pattern of oocyte maturation would explain

the histological appearance of ovaries containing both large numbers of yolked oocytes undergoing α atresia and developing batches of healthy partially-yolked and advanced-yolked oocytes (Fig. 42b).

Later in the season, ovaries occurred in which all oocytes, other than primary growth, were being resorbed through the process of oocyte atresia (Fig. 42a)—indicative of a cessation of spawning. In 1991, this type of atresia first occurred in late June and was common by late August; whereas in 1992, it first occurred and was common by late July. Once ovaries resorbed both yolked and cortical alveolar oocytes, they apparently could not redevelop that spawning season, as I collected no ovaries in the developing stage (Table 11) after the spawning season began in May. However, some ovaries were capable of resorbing all their less-developed oocytes at the same time that they developed and spawned their last batch, as indicated by ovaries which contained only primary growth oocytes, hydrated oocytes, and sometimes β-stage follicular atresia.

Ovarian cycle

Weakfish have a dynamic ovarian cycle. Females enter the general reproductive cycle at the developing stage, either as immature fish develop for the first time, or as sexually mature fish redevelop and leave the resting stage (Fig. 43). At this point, usually in late April/early May,

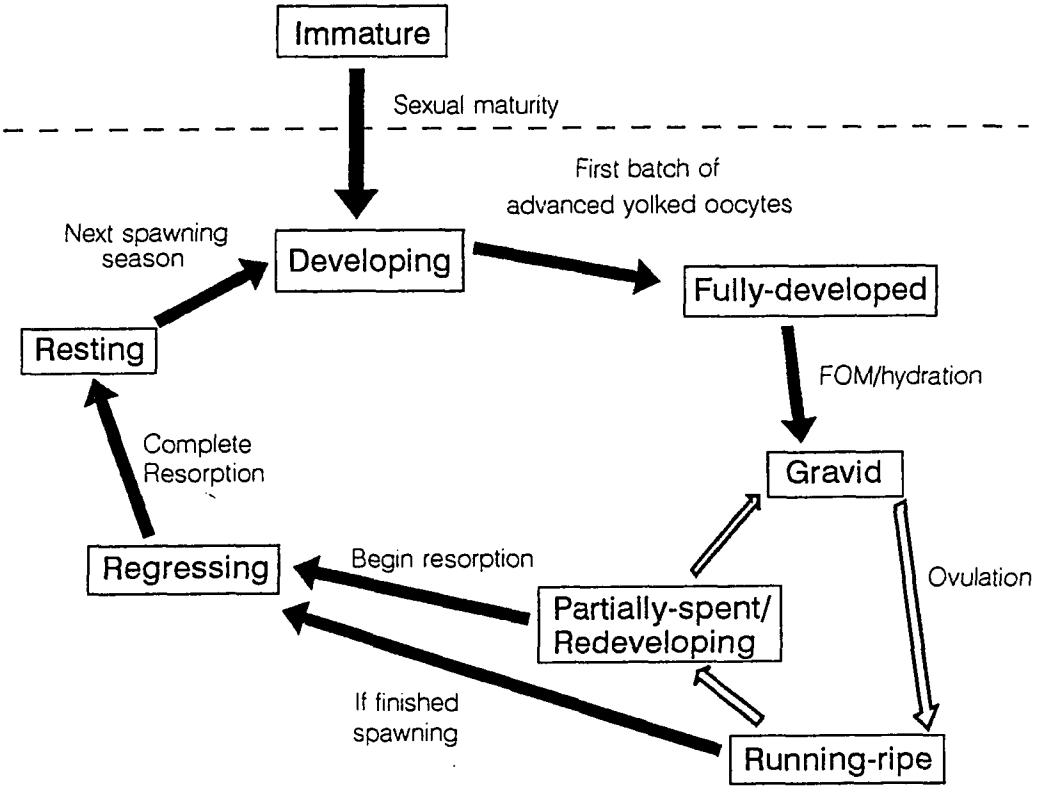
cortical alveolar oocytes and occasional partially-yolked oocytes appear in the ovary. As temperatures warm, development progresses to the fully-developed gonad stage in which females contain advanced-yolked oocytes and can spawn at any time. If the signal for these oocytes to progress to FOM and hence hydration is not received, the most developed oocytes may be resorbed even as more oocytes enter the advanced-yolked stage. However, if the signal is received these fish will enter FOM and progress to the gravid stage, where the ovaries contain hydrated, unovulated oocytes.

Once females have fully-developed ovaries (Table 11) they enter an inner spawning cycle within the general reproductive cycle (Fig. 43). This inner cycle is typical of multiple spawners and consists of ovulation, spawning and redevelopment of partially-spent ovaries to spawn again. In May, when most females are just entering the inner spawning cycle, ovaries and GSIs are at their maximum size.

The rates at which fish move through the inner spawning cycle vary. Some fish can go through it daily, as ovaries containing both degenerating POFs and FOM oocytes indicate. However, most gravid ovaries did not contain degenerating POFs, suggesting that fish usually take at least 2-3 days to complete the cycle. The rates at which fish go through the cycle may also change over the spawning season, as condition and hence energy resources change.

Although vitellogenesis is apparently continuous

Fig. 43. The ovarian cycle of weakfish, showing their general reproductive cycle (solid arrows) and their inner spawning cycle (open arrows), typical of a multiple spawner.


Immature
Sexual maturity
First batch of
advanced yolked oocytes
Next spawning
season
Developing
Fully-developed
Resting
FOM/hydration
Complete
Resorption
Gravid
Regressing
Begin resorption
Ovulation
Partially-spent/
Redeveloping
If finished
spawning
Running-ripe

throughout the spawning season, the number of yolked oocytes within the ovary at any one time decreases as the spawning season progresses. The apparent continuity of vitellogenesis is indicated by the presence of cortical alveoli and partially-yolked oocytes throughout the spawning season, and is typical of a fish with indeterminate fecundity. However, as the spawning season progresses, partially-spent/redeveloping stage ovaries contain fewer yolked oocytes than they did earlier in the season, and GSIs decrease. This decrease in yolked oocytes does not appear to indicate a decrease in spawning activity. For example, mean GSI in August 1991 was the lowest of the spawning season, yet many spawning females occurred. Moreover, ovaries with GSIs as low as 2.3 were found to have remnant hydrated oocytes (Fig. 28b) indicating recent spawning, as well as healthy yolked oocytes.

Fish terminate the inner spawning cycle when their gonads begin to regress, i.e., no longer contain healthy yolked oocytes. The timing of this process, however, is highly variable. Termination of spawning is characterized in the ovaries by one of two histological appearances: (1) all yolked oocytes have become atretic and less-developed oocytes are beginning atresia; or 2) less-developed oocytes are being resorbed as the last batch of late-stage advanced yolked oocytes are developed and spawned. The former pattern appears more common. However, I have observed

several females going directly from the running-ripe to resting ovarian stage.

DISCUSSION

Spawning season, location and pattern

There has been disagreement as to whether weakfish spawn within Chesapeake Bay or off the mouth of the Bay. Pearson (1941) and Massmann et al. (1958) concluded weakfish spawned outside the mouth of the Bay, but Welsh and Breder (1923) and Hildebrand and Schroeder (1928) stated spawning occurred just within the Bay mouth or at its entrance. Olney (1983) concluded weakfish used the lower Bay for spawning, based on numerous collections of early weakfish larvae. However, he could not conclusively demonstrate this, due to the difficulty in identifying sciaenid eggs to the species level.

The occurrence of 20 females in the process of spawning, i.e., running-ripe, collected in this study prove weakfish spawn in the Chesapeake Bay. Although most spawning females came from the lower York River, well within Chesapeake Bay, spawning also occurred at my northern-most station, just south of the Virginia/Maryland border. In addition, the large number of females collected in Chesapeake Bay showing signs of active spawning—gravid

females and females with remnant hydrated oocytes or POFs—coupled with the apparent lack of weakfish spawning in coastal waters off the eastern shore of Virginia (Cowan and Birdsong 1985), suggests weakfish may be predominantly estuarine spawners in the Chesapeake Bay region.

My study indicates weakfish are multiple spawners in the Chesapeake Bay region. The literature, however, is contradictory about whether weakfish are multiple or total spawners, and if this pattern differs within their range. Merriner (1976) first reported multiple spawning of weakfish, in North Carolina waters. He based his conclusion on ovarian characteristics similar to those seen in my study: (1) ripe ovaries also contained less-developed oocytes; (2) partially-spent ovaries occurred regularly in the spawning season; and (3) ripe ovaries became increasingly flaccid and vascularized as the spawning season progressed. Shepherd and Grimes (1984), however, concluded there was no evidence of multiple spawning in Delaware Bay or Gardiners Bay, NY, although they also observed partially-spent ovaries and classified ovaries still containing yolked oocytes as spent. Later, Villoso (1989) found weakfish were multiple spawners in Delaware Bay. Three lines of evidence suggest weakfish are multiple spawners over most of their range (North Carolina to New York): (1) the similarity of Shepherd and Grimes' (1983) oocyte diameter distributions to those presented here; (2) Merriner's (1976) and Villoso's

(1989) conclusions; and (3) the identical appearance of gravid females from Delaware Bay to those from Chesapeake Bay.

The literature is also contradictory over whether weakfish have a shorter spawning season in more northern waters. I found weakfish spawn in Chesapeake Bay from May to August and occasionally to mid-September. These results agree with Merriner's (1976) study from North Carolina, and the reported spawning season of May to September from the Carolinas to Cape Cod (Welsh and Breder 1923, Hildebrand and Schroeder 1928). However, Shepherd and Grimes (1984) reported a shorter spawning season of May to mid-July for the region Delaware Bay north to Long Island, similar to Villoso's (1989) results from Delaware Bay. Shepherd and Grimes (1984) findings disagree, however, with Harmic (1958), Goshorn and Epifanio (1991b) and Paperno (1991), who state weakfish spawn from May to August in Delaware Bay. These disagreements may be due to the fact that Shepherd and Grimes (1984) and Villoso (1989) delineated the spawning season by macroscopic gonad stages and GSIs. Both studies apparently designated as spent, ovaries still containing yolked oocytes, which might have been capable of continued spawning. Because weakfish continue to spawn at low GSIs, the only clear signs that spawning has ended are an absence of healthy yolked oocytes in the ovaries or milt in the testes.

Geographic differences in duration of the spawning season could greatly affect annual fecundity, due to the multiple spawning pattern of weakfish. Thus, although Welsh and Breder (1923) state the weakfish spawning season seems little affected by latitude, further work is needed to determine if fish in more northern estuaries demonstrate shorter spawning seasons.

Sex Ratios

Sex ratios of weakfish collected in Chesapeake Bay during the spawning season by two different gears—gill nets and haul seines—were consistently skewed towards females, at approximately 3:1. The dominance of females found in this study, differs from Shepherd and Grimes (1984), who found roughly a 1:1 sex ratio and from Wilk (1979) who stated that the sex ratio is basically equal and does not differ between areas or years. However, my results are similar to other estuarine studies, e.g., Villoso (1989) found 72% females in May and June 1988 gill net collections in Delaware Bay; O'Reilly (1990) reported 63% females in pound net, gill net and haul seine collections from Chesapeake Bay; and Crozier and Hecht (1914) observed 71% females in July and August pound net collections in Beaufort, NC.

The dominance of female weakfish during summer in estuarine areas could be due to: (1) segregation by sex during spawning, as reported for other species (Hunter and

Goldberg 1980, DeMartini and Fountain 1981, Alheit et al. 1984); (2) increased vulnerability of females to some gears due to increased ovarian development, as suggested by Villoso (1989); (3) sex-specific migration patterns; or (4) a combination of these factors, i.e., spawning groups may be dominated by females and also restricted to certain depths or areas, consequently affecting their vulnerability to different gears.

The female-dominated sex ratios seen in this study cannot be explained solely by increased gear vulnerability of females with increased ovarian development, as a high percentage of females occurred in September and October 1990 and 1991 after spawning ended, and fewer females than males were collected in May 1990, when spawning began. Instead, different proportions of the sexes may actually enter estuarine spawning grounds than occur in coastal waters. This might explain the sex ratios closer to 1:1 seen in my North Carolina shelf water collections, as well as those reported by Shepherd and Grimes (1984) and Wilk (1979)—since both their studies relied heavily on coastal trawling conducted by the National Marine Fisheries Service.

Size and age at maturity

I found most weakfish in Chesapeake Bay were sexually mature by age 1. Merriner (1976) and Shepherd and Grimes (1984) also reported most weakfish reach maturity by age 1

in North Carolina and New York, respectively. Merriner (1976) found males mature at 157-181 mm TL and females at 175-230 mm TL, similar to my L_{50} results of 164 mm TL for males and 170 mm TL for females. Shepherd and Grimes (1984), however, found somewhat larger mean sizes at maturity, 251 mm TL for males and 256 mm TL for females.

Although most weakfish in Chesapeake Bay mature by age 1, some age 1 fish apparently do not mature until the middle of the spawning season. Merriner (1976) also noted this pattern in North Carolina, where weakfish born in May or June mature by the next May or June, but those born in July or August do not mature until late the following summer. Thus, spawning patterns in the previous year, i.e., whether spawning was more intense early or late in the season, affects the egg production of age 1 fish. This could have an important effect on the population's egg production, since the greater numbers of age 1 fish may offset their lower batch fecundities.

Diel Periodicity

Weakfish spawn at dusk in the Chesapeake Bay and apparently throughout their range. I collected gravid females, just prior to spawning, primarily between 1700-2000 hrs. Welsh and Breder (1923) stated, based on the relative number of eggs collected at different times of day, that weakfish spawn at night and predominantly in the early

evening. More recently, Ferraro (1980) found weakfish spawn in Peconic Bay, NY at approximately 1800 hrs and Villoso (1989) found they spawn in the Delaware Bay between 1700 and 1900 hrs. Goshorn and Epifanio (1991b) reported that when weakfish gametes were stripped into a bucket of seawater, fertilization only occurred between 1800-2100 hrs.

The rapid progression from hydration to ovulation and extrusion I found in weakfish was also reported by Villoso (1989). Weakfish oocyte development from FOM to hydration and ovulation is similar to that described for spotted seatrout, Cynosion nebulosus, in the Gulf of Mexico (Brown-Peterson et al. 1988). Villoso (1989) also reported the retention of ovulated, hydrated oocytes by hormonally-treated female weakfish for 2-4 days after ovulation. After day 3, he found many of them became atretic and collapsed in appearance. However, it is not known how common retention of hydrated oocytes is, what causes this, or how long these oocytes remain viable.

Gear selectivity occurs due to the diel periodicity of weakfish spawning and possibly also due to the different depths and habitats gears exploit (Higgins and Pearson 1928). Most of the hydrated females I collected (75%) came from gill nets, even though this gear provided only 26% of the total females. Pound nets and haul seines undersample hydrated females because their catch is generally killed at dawn and weakfish spawn at dusk. They also sample fish at

different depths, with pound net lead lines often set in channels 7.5-12 m deep and haul seines fishing in water < 3 m. In order to better understand how different gears are biased in terms of weakfish reproductive studies, it will be necessary to more specifically delimit the depths and habitats in which weakfish spawn.

Age composition of spawning population

I found no evidence that larger, older fish spawn over a longer time period than smaller fish. Other than age one fish, females of all ages had developing ovaries with yolked oocytes in April and were fully-developed by May. In contrast, Shepherd and Grimes (1984) and Villoso (1989), based on GSI data, reported that larger fish develop earlier. However, GSIs are not good predictors of developmental stage and are not independent of fish size (West 1990). Although I found some fish ages 1-5 spawning through mid-August, it is unclear how the migrational pattern affects the spawning of older fish, i.e., fish older than age 3 occur in Chesapeake Bay predominantly in April and May (Chapter 2) before most spawning has begun.

Spawning activity and fecundity

I found weakfish spawning activity in Chesapeake Bay varied both within the spawning season and between years.

In 1991, spawning females were relatively common from mid-May through June, scarce in early July, and again common from the last week of July through August. Welsh and Breder (1923) and Harmic (1958), both reported two waves of weakfish spawning, one in June and the other in late July—similar to the pattern seen in 1991—and numerous studies have reported a bimodal length distribution of juvenile weakfish (Massmann et al. 1958, Thomas 1971, Merriner 1973, Shepherd and Grimes 1983).

In 1992, however, the number of spawning females again declined in July, but there was little recovery later in the season, suggesting the timing and magnitude of spawning varies greatly from year to year. Similarly, Szedlmayer et al. (1990), based on daily ageing, found a different pattern of brithdate frequency distributions in 1983 than in 1984. In 1983, Szedlmayer et al. (1990) reported three spawning waves: one from June through mid-July, a second from mid-July through mid-August, and a third much smaller wave from mid-August through mid-September. In 1984, however, he reported two major spawning waves with a break in late June/early July comparable to the pattern I found in 1991. Olney (1983) also reported annual variation in weakfish spawning. Pearson (1941) in 1929 and 1930 found weakfish larvae in the lower Bay most abundant in June and virtually absent in August—similar to the spawning pattern I saw in 1992. Whereas, Olney (1983) in 1971-1973 found peak

abundance of weakfish larvae in the lower Bay to occur in August.

Neither the lunar cycle nor water temperature explained the changes in spawning activity I observed. Although a good correlation between the phases of the moon and spawning activity has been reported for other species (e.g., California grunion, Leuresthes tenuis, (Clark 1925); the queenfish, Seriphus politus, (DeMartini and Fountain 1981); mummichog, Fundulus heteroclitus, (Taylor et al. 1979)), it does not explain either the within-season or annual variation I observed in weakfish spawning activity. Neither does water temperature. As Harmic (1958) stated, the weakfish pattern of spawning activity is difficult to correlate with temperature—since once a certain threshold temperature is reached, spawning should occur, as long as temperatures do not fall below the threshold level. Although there could also be an upper threshold, above which spawning does not occur, this does not appear to be the case, as spawning activity decreased in July of 1991 and 1992, even though temperatures were considerably lower in 1992.

Food supply, however, may explain within-season and interannual spawning patterns. Because oocyte growth and somatic growth are affected by the same factors, i.e., food and metabolic hormones (Cushing 1990), the nutritional state of spawners should affect egg production (Houde 1989). The

relatively long spawning season and potentially high spawning frequency of weakfish suggest energy reserves and food availability may limit total egg production—as suggested for two other marine multiple spawners, the northern anchovy, Engraulis mordax, (Hunter and Goldberg 1980, Hunter and Leong 1981), and the queenfish (DeMartini and Fountain 1981). The higher percentage of weakfish with empty stomachs in July/August of 1992 than in 1991, and the fewer spawning females seen in 1992, as well as the similarity between temporal patterns of mean monthly condition and occurrence of spawning females indicate a relationship between spawning activity and food supply. Hislop et al. (1978) reported that condition factors of haddock, Malanogrammus aeglefinus, increased with energy intake, and that spawning was reduced in fish fed low rations. Wootten (1977) also found that the percentage of spawning female sticklebacks, Gasterosteus aculateus, increased with ration size, but that batch fecundity did not—similar to the same batch fecundity-at-size, but lower spawning frequencies, I found for weakfish in 1992.

In general, spawning frequencies are difficult to determine in marine multiple spawners with asynchronous oocyte development (Brown-Peterson 1988). Spawning frequencies estimated from the percentage of hydrated females on the spawning grounds may be overestimates, if the percentage of fish spawning in these areas is higher than

that of the population. An additional problem is a potential relationship between catchability and spawning activity, i.e., if fewer fish are caught during times of low spawning activity. If this relationship exists, then both methods could potentially overestimate spawning frequency. Also the spawning frequencies I present represent how often, on average, females spawn throughout the spawning season. While appropriate for annual fecundity estimates, this does not reflect how frequently fish spawn at any given time. For example, in May and June weakfish may have spawned as frequently in 1992 as in 1991, but the 1992 annual spawning frequency was lower because spawning activity decreased later in the season.

Although lower in 1992 than 1991, my estimates of annual fecundity were an order of magnitude greater than previous estimates based on the assumption of determinate fecundity (Merriner 1976, Shepherd and Grimes 1984, Villoso 1989). Such large discrepancies between estimates based on determinate versus indeterminate fecundity are not uncommon for marine multiple-spawning fish (DeMartini and Fountain 1981). Given the comparable abundance of weakfish larvae taken in the summer in the lower Bay (Pearson 1941, Olney 1983) to the highly fecund, ubiquitous bay anchovy, Anchoa mitchilli—which also spawns from May to August (Luo and Musick 1991)—my higher fecundity estimates appear appropriate.

It is not clear how common large fluctuations are in interannual fecundity of marine multiple spawners—such as I saw in 1991 versus 1992. Fecundity estimates for more than one year are rarely reported for marine multiple spawners (DeMartini 1990). However, Lasker (1985) pointed out that northern anchovy reproduction was very dynamic and that egg mortality, batch fecundity and spawning frequency varied greatly from year to year.

Effects of weakfish reproduction on year-class strength

An increased food supply may have increased weakfish egg production during the early 1970's. Both Rothschild (1981) and Verity (1987) pointed out that abundance of Atlantic menhaden, Brevoortia tyrannus—a common forage fish of weakfish—increased in the Chesapeake Bay in the 1970's, as weakfish abundance also increased. Joseph (1972) reported very low abundance of weakfish larvae in Chesapeake Bay in the 1960's, stating that extensive ichthyoplankton studies seldom obtained more than one weakfish larva/tow. Whereas, Olney (1983) found weakfish to be second in abundance only to the bay anchovy in 1971-1973.

Weakfish egg production will not be directly proportional to spawning stock biomass if it is affected by food availability. Thus, a given fishing mortality could affect egg production differently in different years, and egg production, not spawning stock biomass, should be

considered in analyses of recruitment variability (Rothschild and Fogarty 1989).

Because the relationship between weakfish egg production and year-class strength is unknown, its importance in the recovery of the weakfish fishery in the 1970's cannot be determined. Joseph (1972) hypothesized the weakfish abundance in the 1950's and 1960's was due to reproductive failure, noting the sharp decrease in Chesapeake Bay larval abundance in the early 1960's, compared to 1929 and 1930 (Pearson 1941). Although larval abundance recovered in the 1970's (Olney 1983), concurrent with the recovery of the fishery (Mercer 1985, Chapter 2), trawl survey indices of juvenile abundance in the York River, VA, 1955-1982 (Mercer 1985) did not show a similar large increase in the late 1960's/early 1970's.

The dynamic pattern of weakfish reproduction affects adult populations in several ways. The extended spawning season in Chesapeake Bay, May-August, insures larvae are born into different environmental conditions, with early-born weakfish having greater opportunity for growth before their first winter than fish born later. Thus, time of birth may affect size-at-age and size-related mortality. In addition, time of peak spawning may affect recruitment if different mortality rates are associated with early versus late birthdates as Paperno (1991) suggested. Birthdate also affects whether age 1 fish mature at the beginning of the

spawning season or at mid-season, thus affecting population egg production.

CHAPTER 4

Yield-per-recruit modeling

INTRODUCTION

Yield-per-recruit models assess the balance between growth, natural mortality and fishing mortality to determine how these factors affect the biomass of the fishable portion of a stock. These models assume that: (1) the fishery and the stock are in equilibrium; (2) growth and mortality parameters remain constant over the range of conditions examined; and (3) recruitment is constant (Ricker 1975). Although these assumptions are limiting, yield-per-recruit models have been widely used in fish population dynamics studies (Beverton and Holt 1957, Ricker 1975, Gulland 1983) because they allow easy evaluation of the response of yield to important management parameters, i.e., changes in fishing mortality and age at first capture (Huntsman et al. 1983).

Though yield-per-recruit analysis is an important basis for scientific advice to management (Deriso 1987), it has rarely been applied to weakfish—primarily because of a lack of data (Mercer 1985). Boreman and Seagraves (1984) applied a Thompson and Bell model, concluding that weakfish from Maryland to North Carolina were growth overfished. However, as they and Mercer (1985) pointed out, data weaknesses and a lack of knowledge of stock structure made these conclusions

questionable. Ricker yield-per-recruit models have also been applied by Hawkins (1988) and Vaughan et al. (1991). They found that increasing size at first capture would increase yield-per-recruit. However, no published yield-per-recruit analyses exist for weakfish.

In this chapter I use the Beverton-Holt yield-per-recruit model (Beverton and Holt 1957) to assess the effect of different fishing mortality and age at first capture schedules on weakfish yields. I also use the Ricker model to evaluate cohort biomass-at-age (Ricker 1975) for different levels of fishing mortality and age at first capture. Management implications of these simulations and their limitations are discussed.

MATERIAL AND METHODS

Yield-per-recruit calculations

Yield-per-recruit analysis was based on the Beverton-Holt model (Beverton and Holt 1957), using the following equation:

$$Y/R = Fe^{-M(t_c - t_r)} W_\infty \sum_{n=0}^{3} \frac{U_n e^{-nK(t_c - t_0)}}{F+M+nK}$$

where:

Y/R = yield-per-recruit

F = instantaneous rate of fishing mortality

M = instantaneous rate of natural mortality

W_∞ = asymptotic weight

U_n = summation parameter, where $U_0=1$, $U_1= -3$, $U_2=3$, $U_3= -1$

t_c = age at first capture

t_r = age at recruitment to the fishing area

K = the Brody growth coefficient

Changes in cohort biomass-at-age, at different levels

of F, were examined using the Ricker model:

$$\overline{B_t} = \frac{B_t(1+e^{G_t-(M_t+F_t)})}{2}$$

where:

t = a selected time interval

B_t = arithmetic mean biomass of the stock during t

B_t = biomass of the stock at the beginning of t

G_t = instantaneous rate of growth during t

M_t = instantaneous rate of natural mortality during t

F_t = instantaneous rate of fishing mortality during t.

The computer program B-H3 was used to calculate Beverton-Holt yield-per-recruit, and the computer program Ricker was used for cohort biomass-at-age. Both programs are in the Basic Fisheries Science Programs package (Saila et al. 1988)

Parameter estimates

Parameter values used in yield-per-recruit simulations are summarized in Table 17. Growth parameter estimates (L_∞, K, and t_0) were obtained from the von Bertalanffy equation in Chapter 2. W_∞ was estimated from the asymptotic length, L_∞, using the somatic weight to total length relationship for pooled sexes in Chapter 2.

An upper limit to M was calculated using the following equation, based on the reasoning of Royce (1972):

$$S = e^{-Ztmax}$$

where:

S = survival rate, assumed to be 0.01 at maximum age

Z = instantaneous total mortality rate

t_{max} = maximum age.

A t_{max} of 17-years-old was used, as this is the oldest weakfish ever reported (Chapter 2). Under these conditions Z equaled 0.27. Given that an estimate of instantaneous total mortality, based on the maximum age of a lightly fished stock, should approximate M (Beverton 1963), I assumed M was less than 0.27, since the weakfish stock was heavily exploited during the 17-year-old's lifespan (Mercer 1985).

My best estimate of weakfish natural mortality was M=0.20. This was based on the general relationship between growth and natural mortality (Beverton 1963, Gulland 1983), and the numerous examples in fisheries literature where M approximates K (Alverson and Carney 1975)—my estimate of K being 0.17. In addition, this level of M corresponds to a maximum lifespan of 23 years, which appears reasonable. However, Y/R simulations were conducted over a range of M's

Table 17. Parameter estimates or range of values used in yield-per-recruit simulations for weakfish in Chesapeake Bay

Parameter	Estimate	Method	Value or range used in simulations
K	0.17	growth curve[1]	0.17
W_∞	9526.70 g	converted from L_∞[1]	9526.70 g
t_0	-0.18	growth curve[1]	-0.18
t_r	0	life history information[2]	0
t_c	2	age composition of catches[1]	1 - 12
F	-	-	0 - 2.5
M	maximum of 0.27	longevity[3]	0.1 - 0.25

[1]Chapter 2; [2]Chapter 3; [3]Royce (1972)

from 0.1 to 0.25, which correspond to a maximum lifespan of 18 to 46 years.

Because it was not possible to estimate current Z, it was also not possible to estimate current F. However, based on a probable range of Z of 0.38-0.77 (Chapter 2), the simulated range of M, and the equation: F=Z-M, a range of possible current instantaneous fishing mortality was calculated as 0.13-0.67.

The estimated age at recruitment to the exploited region, t_r, of 0 is based on reports of spawning, early life history stages, and juveniles occurring in Chesapeake Bay (Massmann et al. 1958, Chao and Musick 1977, Olney 1983, Szedlmeyer et al. 1990, Chapter 3). Current age at first capture, t_c, was based on age compositions for commercial grade pound net, haul seine and gill net catches in Chesapeake Bay for the period 1989-1992. Although yearlings are exploited, 2-year-olds are the first age-class fully-recruited to the commercial foodfish grades (Chapter 2).

The proportion of the potential growth span remaining when fish enter the exploited phase of life, was calculated using the equation: $1 - L_c/L_\infty$ (Beverton 1963). My estimate of L_c, the average length at first capture, was obtained by converting t_c, mean age at first capture, to lengths predicted from the von Bertalanffy equation. My estimate of L_∞ was also from the von Bertalanffy equation.

For Ricker cohort biomass-at-age curves, t was set at

an interval of one year. Mean somatic weight-at-age (SW_t) was calculated from lengths-at-age predicted from the von Bertalanffy growth curve and converted to somatic weight using the somatic weight to total length relationship for pooled sexes (Chapter 2). The instantaneous rate of growth, G_t (Ricker 1975), was calculated as: $\ln SW_{t+1}/SW_t$. Annual fishing and natural mortality rates were kept constant throughout a cohort's lifespan. I assumed M=0.20, and evaluated a range of F's: 0.00, 0.10, 0.25, 0.50, 0.75, 1.00, 1.25, and 1.50 for t_c=2-5.

Maximum yield-per-recruit of a cohort occurs when the cohort reaches their "critical size", t_{critic}, where the instantaneous growth rate equals the instantaneous natural mortality rate (Ricker 1975). Management measures to maximize yield-per-recruit attempt to yield fish whose average size approximates t_{critic} (Alverson and Carney 1975). I estimated t_{critic} following Alverson and Carney (1975) and Deriso (1987) as:

$$t_{critic} = t_0 + \frac{1}{K}\ln(3K/M+1)$$

using t_0 and K from the von Bertalanffy equation and M=0.20.

RESULTS

Yield-per-recruit analysis

Weakfish Y/R isopleths indicate maximum yields occur at high t_c and F (Fig. 44). Maximum yield occurred at F=2.5 and t_c=10, 8, 7, and 6 for M=0.10, 0.15, 0.20, and 0.25, respectively. For all levels of M, at t_c less than that of maximum yield, yield rapidly increased at very low levels of F and then decreased as F increased. This is indicated by the downward dip of the yield isopleths at F < 0.5. The level of M did affect the magnitude and maximum values of Y/R and the optimum t_c, with both yield and optimum t_c decreasing as M increased. However, M had little affect on the relative pattern of the isopleths.

These same patterns can be seen more easily in plots of Y/R on F. Regardless of M, Y/R curves at t_c < 4 peak at low F and then decline at higher F (Figs. 45, 46, 47, & 48). Thus, for a low t_c, there is a level of fishing above which yield decreases. For example, at M=0.20 and the current t_c=2 (Fig. 47), maximum yield occurs at F=0.20. However, potential yield is reduced by 23% by F=0.60—a level within the probable range of F (0.13-0.67). The percent reduction

Fig. 44. Weakfish yield-per-recruit isopleths, estimated for t_c=1-12, F=0.0-2.5, and M=0.10-0.25.

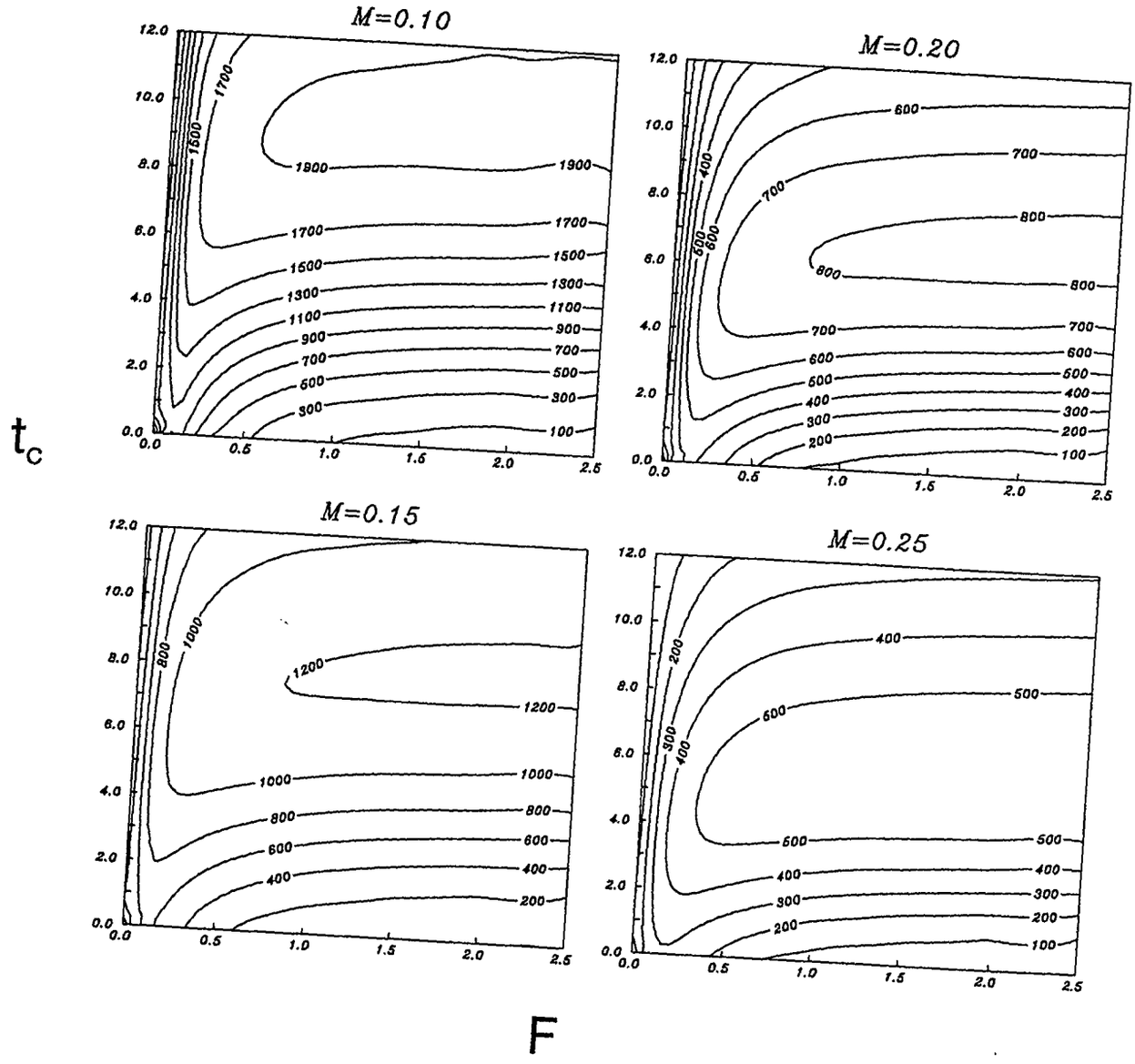

M=0.10
M=0.20
M=0.15
M=0.25
t_c
F

Fig. 45. Weakfish curves of yield-per-recruit on F, estimated for t_c=1-12, F=0.0-2.5 and M=0.10. Triangles indicate F_{Max}.

M = 0.10

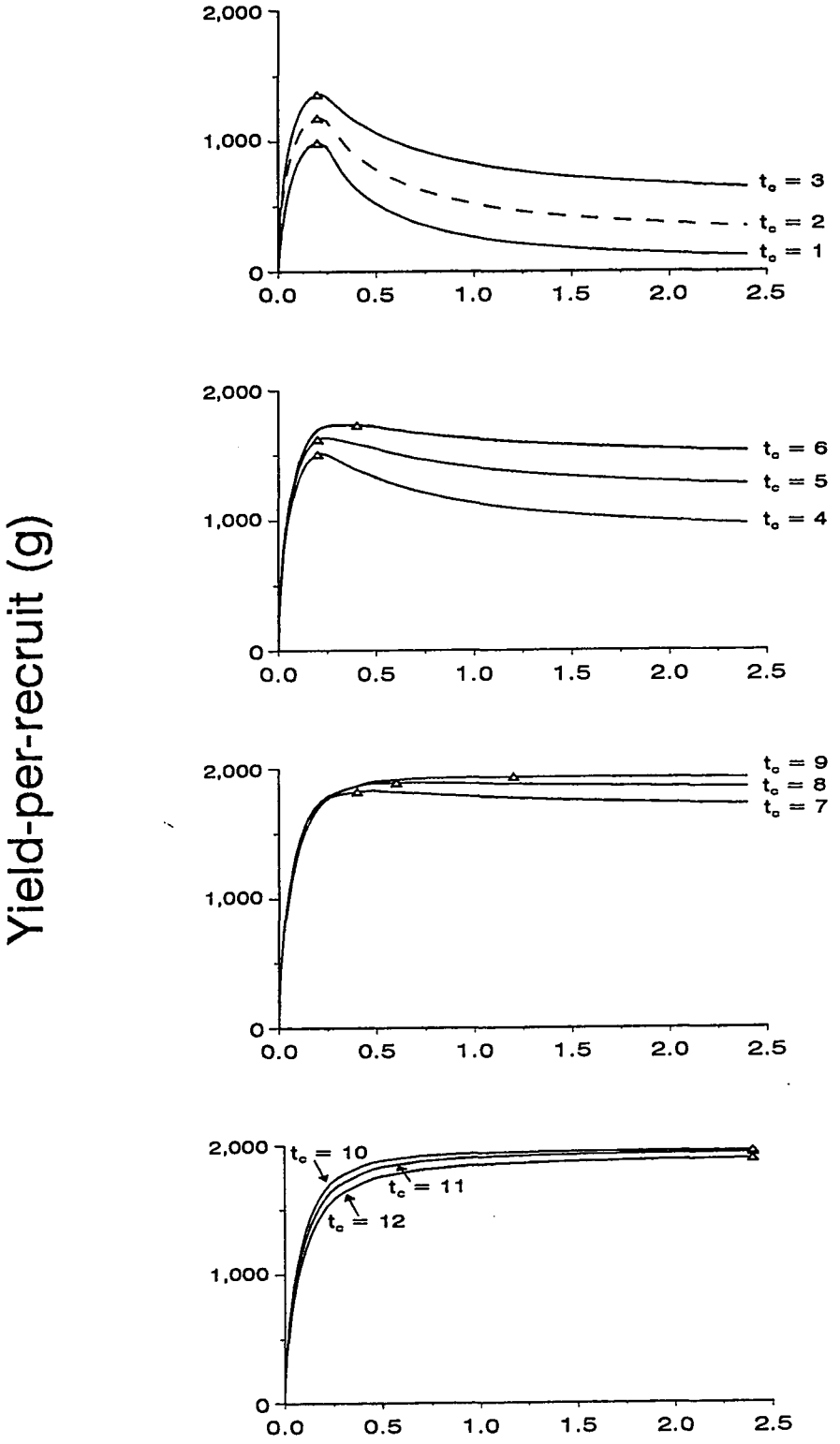

Yield-per-recruit (g)
2,000
1,000
0
0.0
0.5
1.0
1.5
2.0
2.5
t_c = 3
t_c = 2
t_c = 1
t_c = 6
t_c = 5
t_c = 4
t_c = 9
t_c = 8
t_c = 7
t_c = 10
t_c = 11
t_c = 12
F

Fig. 46. Weakfish curves of yield-per-recruit on F, estimated for t_c=1-12, F=0.0-2.5 and M=0.15. Triangles indicate F_{Max}.

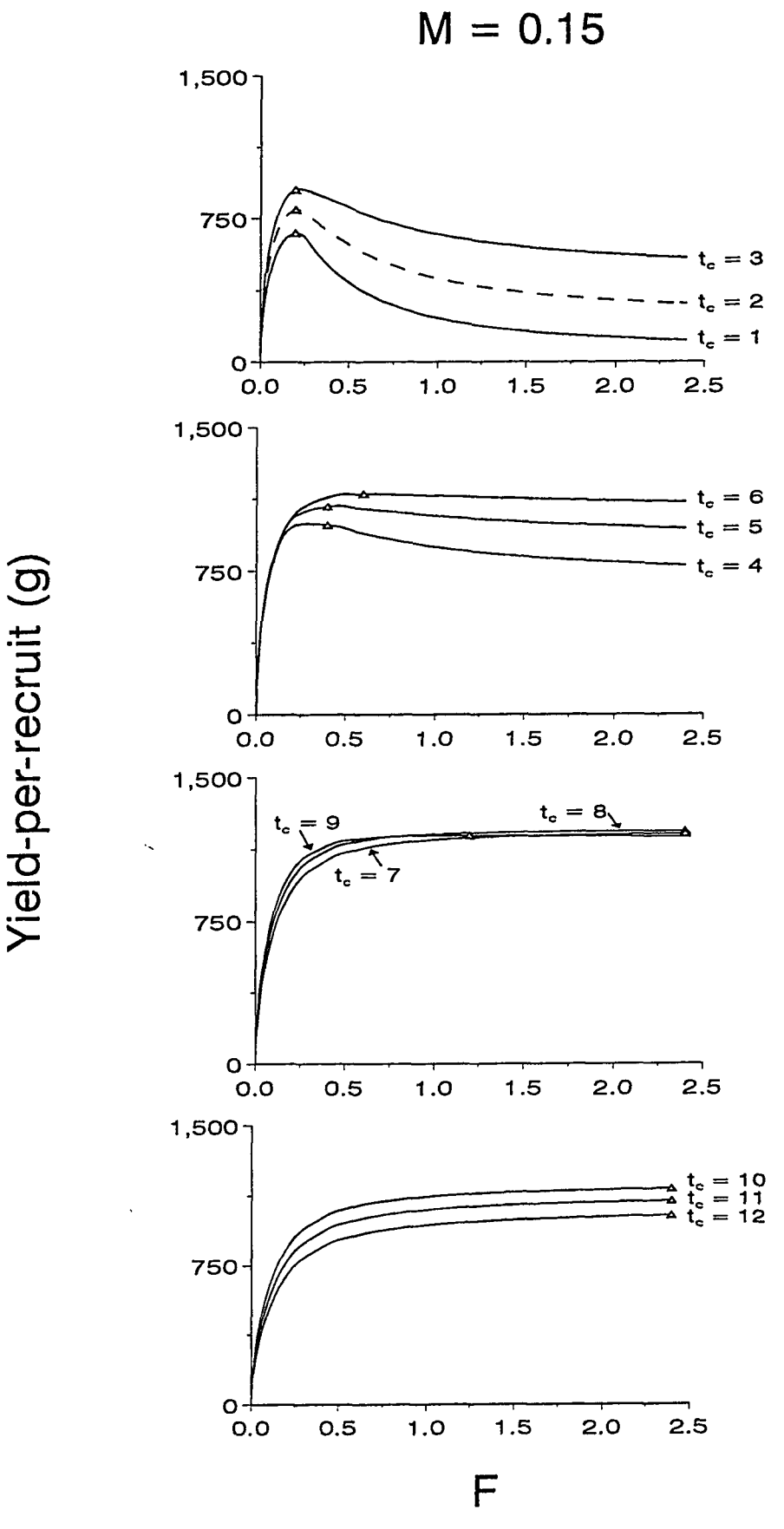

M = 0.15
Yield-per-recruit (g)
F
1,500
750
0
0.0
0.5
1.0
1.5
2.0
2.5
$t_c = 3$
$t_c = 2$
$t_c = 1$
$t_c = 6$
$t_c = 5$
$t_c = 4$
$t_c = 9$
$t_c = 8$
$t_c = 7$
$t_c = 10$
$t_c = 11$
$t_c = 12$

Fig. 47. Weakfish curves of yield-per-recruit on F, estimated for t_c=1-12, F=0.0-2.5 and M=0.20. Triangles indicate F_{Max}.

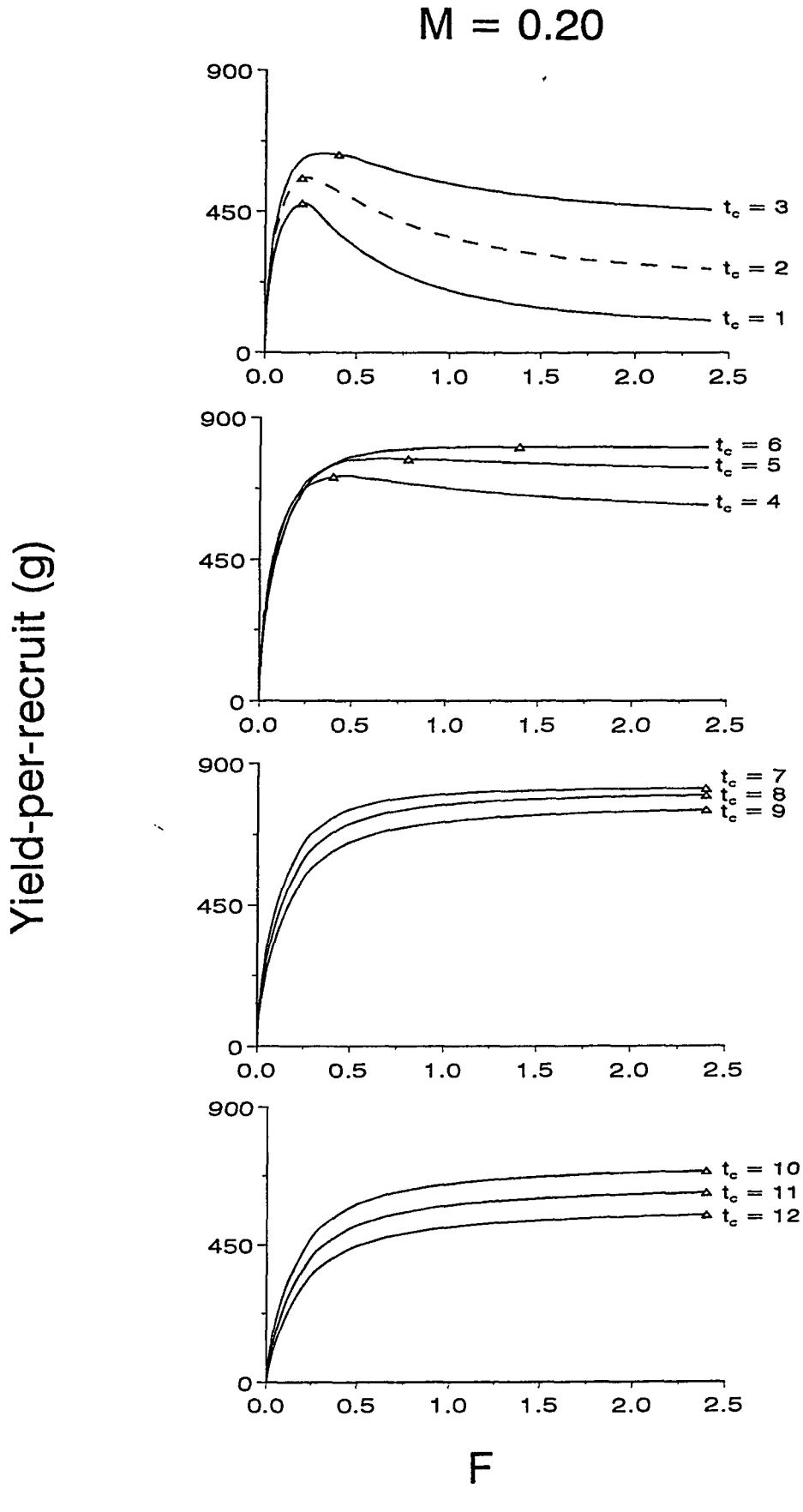
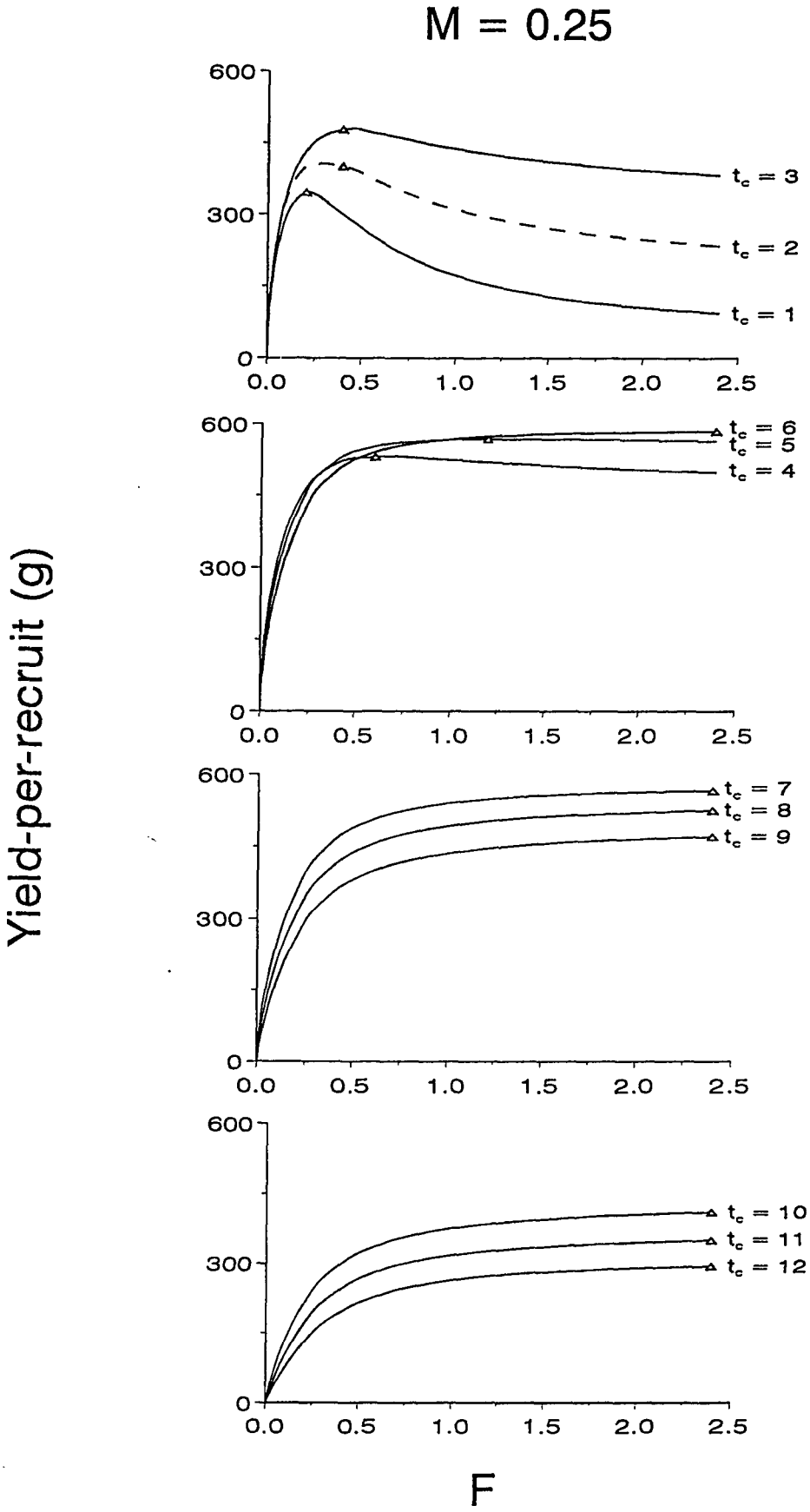

M = 0.20
Yield-per-recruit (g)
F
900
450
0
0.0
0.5
1.0
1.5
2.0
2.5
t_c = 3
t_c = 2
t_c = 1
t_c = 6
t_c = 5
t_c = 4
t_c = 7
t_c = 8
t_c = 9
t_c = 10
t_c = 11
t_c = 12

Fig. 48. Weakfish curves of yield-per-recruit on F, estimated for t_c=1-12, F=0.0-2.5 and M=0.25. Triangles indicate F_{Max}.


M = 0.25
Yield-per-recruit (g)
600
300
0
0.0
0.5
1.0
1.5
2.0
2.5
$t_c = 3$
$t_c = 2$
$t_c = 1$
$t_c = 6$
$t_c = 5$
$t_c = 4$
$t_c = 7$
$t_c = 8$
$t_c = 9$
$t_c = 10$
$t_c = 11$
$t_c = 12$
F

is even greater at lower levels of M and t_c (Figs. 45 & 46), and the reduction increases with F at all levels of M.

As t_c increases, Y/R curves become more asymptotic—indicating at high t_c, similar yields will be obtained over a broad range of F. F at maximum yield (F_{Max}) occurs at higher levels of F as M increases. F_{Max} occurred at 2.5 (the maximum simulated F) at t_c=10, 8, 7, and 6 for M=0.10, 0.15, 0.20, and 0.25, respectively (Figs. 45, 46, 47, & 48). Thus, the potential for growth overfishing from too high a level of fishing pressure decreases as t_c and M increase.

An appropriate range of t_c to maximize yield would be ages 4-6, depending on the actual level of M. Yield was less than the maximum potential when t_c was ≤ age 7, over the range of simulated M. Maximum yield occurred at t_c=10, 8, 7, and 6 for M=0.10, 0.15, 0.20, and 0.25, respectively (Figs. 45, 46, 47, & 48). For M=0.10 and 0.15, yields at t_c=6 are greater than yields at lower t_c at all levels of F (Figs. 45 & 46). However, at M=0.20 and 0.25, yields at t_c=6 are higher than at t_c=4-5 only at higher levels of F (Figs. 47 & 48). This range of appropriate t_c corresponds to an L_c range of 500-640 mm TL.

The amount of growth overfishing currently occurring depends on the level of M. As with growth overfishing due to an excessive F, growth overfishing due to an insufficient t_c will be greatest if M is at the low end of the simulated range. This is indicated by the increasingly asymptotic

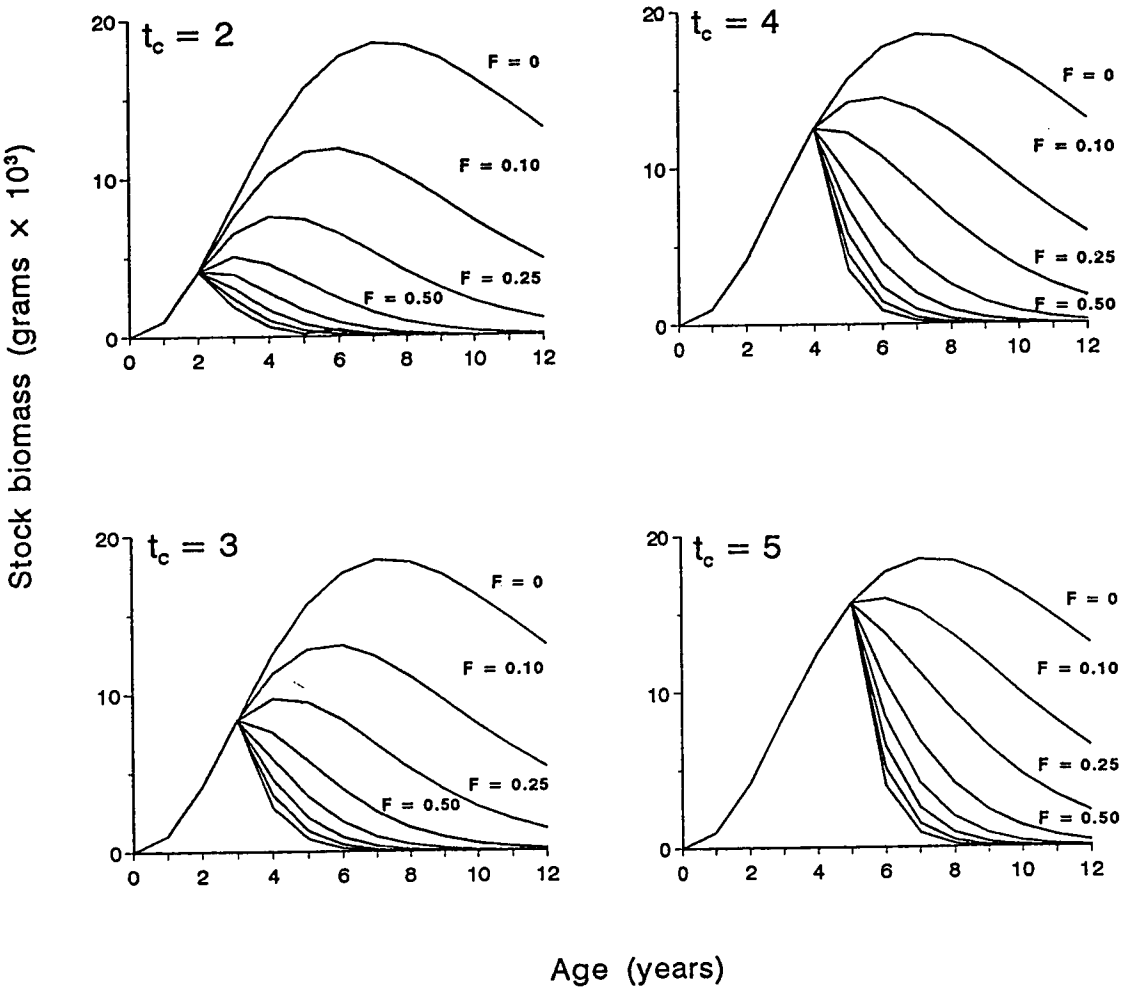
curves at lower t_c as M increases (Figs. 45, 46, 47, & 48). For M=0.20, maximum potential yield increased by 14%, 28%, 38%, and 45%, and F_{Max} increased to 0.40, 0.40, 0.80, 1.40 as t_c was raised from the current level of 2 to ages 3, 4, 5, and 6, respectively (Fig. 47). Actual gains in potential yields would probably be greater, assuming current F > 0.20, the level of F_{Max} at t_c=2.

Cohort biomass

Weakfish reach maximum theoretical cohort biomass at age 6 or older. Values of t_{critic} were: 10.3, 8.4, 7.2, and 6.3 years for M=0.10, 0.15, 0.20, 0.25, respectively. At the current t_c=2, weakfish still have 69% of their potential growth span remaining when they are first harvested.

Because weakfish grow fairly slowly, they are sensitive to growth-overfishing and stock juvenescence. Ricker analysis indicates virgin maximum cohort biomass is achieved at age 7. As F is introduced and increases, age at maximum cohort biomass decreases. At current t_c=2, the age at maximum cohort biomass decreased from age 6 to 2, as F increased from 0.10 to 0.75 (Fig. 49). Similarly, maximum cohort biomass decreased: at the lowest simulated F (0.10), maximum cohort biomass was only 64% of that in a virgin stock, and it was only 22% by F=0.75. The age structure of the stock also changes as F is introduced. Fish > age 8 are 39% of the virgin cohort biomass (Fig. 49). However, at the

Fig. 49. Ricker biomass-at-age estimates for a hypothetical weakfish year-class at M=0.20 and F=0.00, 0.10, 0.25, 0.50, 0.75, 1.00, 1.25, and 1.50 for four levels of t_c: 2, 3, 4, and 5.


Stock biomass (grams x 10³)
$t_c = 2$
$t_c = 3$
$t_c = 4$
$t_c = 5$
F = 0
F = 0.10
F = 0.25
F = 0.50
0
10
20
0 2 4 6 8 10 12
Age (years)

current t_c=2, and F=0.10 these older fish have been reduced by 57%, and by F=0.75, they are basically nonexistent. The effect of F on maximum cohort biomass and age structure, however, is decreased as t_c increases.

DISCUSSION

Yield-per-recruit analysis demonstrated that over a reasonable range of natural mortality, growth overfishing is occurring in the Chesapeake Bay at the current estimated t_c of 2-years-old. Weakfish yield-per-recruit isopleths showed increased potential yield-per-recruit for older ages at first capture (t_c=3-6) for all levels of F and M, indicating that too many fish are being captured before they have had enough time to grow to a more optimal size.

Yield-per-recruit on F plots demonstrated that weakfish yield can be maximized by raising the age at first capture or by keeping fishing mortality low. This effect of fishing pressure is typical of species vulnerable to growth overfishing, i.e., fish with slow growth and low mortality (Gulland 1983). Biomass-at-age plots show that even low levels of fishing mortality (F=0.10) can be expected to cause juvenescence of the weakfish age structure at the current estimate of t_c=2 and that by F=0.75, juvenation of the stock (Ricker 1975) has occurred, with almost no fish older than age 8 surviving.

However, the degree of growth-overfishing currently

occurring may be greater than indicated for t_c=2. I consider t_c=2 an overestimate in Chesapeake Bay for the following reasons: (1) it was based on commercial market grades instead of overall catches and weakfish have been shown to make up a large portion of the Chesapeake Bay pound net scrap fishes (McHugh 1960); (2) the high number of yearlings sampled in the commercial foodfish grades in 1990 (Chapter 2); and (3) the small size (< 300 mm TL) of weakfish vulnerable to haul seines and pound nets (Chapter 2). However, whether t_c is age 2 or lower, will only affect the relative degree of growth overfishing, as can be seen by the plots of yield-per-recruit on F, with yield being maximized at t_c=6—considerably older than age 2—regardless of the level of M or F.

However, the conclusions of the current modeling must be evaluated in terms of their applicability to the general weakfish population (Vaughan et al. 1991). Although several studies have concluded there were multiple stocks of weakfish in the Middle Atlantic region (Perlmutter et al. 1956, Seguin 1960, Shepherd and Grimes 1983), more recent studies have found no such stock structure (Crawford et al. 1988, Hawkins 1988, Graves et al. 1992, Chapter 2). These more recent studies have indicated that the Mid-Atlantic fisheries exploit a common group of weakfish (Hawkins 1988). The biological estimates used in the current Y/R analysis should be applicable to the stock, since reported growth and

longevity from North Carolina (Hawkins 1988) to Delaware Bay (Villoso 1989) is similar to that in Chesapeake Bay (Chapter 2). In addition, the coastwide estimate of t_c=1 (Boreman and Seagraves 1981) suggests weakfish are being growth overfished throughout their range, although the parameters t_c and F may vary regionally.

Even though the general conclusion that weakfish are being growth overfished at t_c < ages 4-6 is well-founded, more precise conclusions as to the optimal t_c and F are difficult to make due to data limitations. The theoretical optimum t_c and F will depend on M. However, M cannot be well-defined until coastwide estimates of Z and F have been determined. In addition, although a range of probable F was presented (0.13-0.67) it is too broad to determine if yield is currently being maximized at t_c=2, since F_{Max} occurs at F=0.20.

Additional problems in applying these modeling results to management decisions arise due to model limitations, the multispecies nature of the fishery and the complicated migrational pattern of weakfish. Management of weakfish based on fishing mortality rates will be difficult, if not impossible, because of: (1) insufficient catch and effort data (Mercer 1985); (2) no current estimates of F; and (3) an incomplete understanding of the relationship between fishing mortality and fishing effort. Management strategies based on age at first capture, on the other hand, would seem

a simple matter—especially considering the strong effect of t_c on weakfish yield-per-recruit. However, the weakfish migrational pattern complicates the issue.

Although age at first capture may be similar coastwide, the amount of fishing pressure on younger weakfish is not. North Carolina catches are dominated by fish ages 0-2 (Hawkins 1988), Chesapeake Bay catches consist primarily of ages 1-4 (Chapter 2) and at least in the past, New York/New Jersey fisheries were dominated by fish ages 3 or older (Perlmutter et al. 1956, Joseph 1972). Thus, even though a $t_c \geq 4$ might be best for the overall yield of the stock, it would most likely mean closing the North Carolina inshore and Chesapeake Bay fisheries. Additionally, the multispecies nature of these fisheries makes such a high t_c impractical as the mesh size necessary to increase the weakfish t_c to $\geq$ age 4 would also exclude smaller species such as croaker and spot. Another problem concerning weakfish age at first capture is the bycatch of young weakfish (age 0 and 1) in the South Atlantic shrimp fishery and its impact on the stock (Vaughan et al. 1991).

There are also limits to the Y/R models and the information their application can offer (Ricker 1975, Gulland 1983, Neilson and Bowering 1989). The most obvious of these are: (1) the assumption of steady state; (2) the single species approach; and (3) the lack of information on how fishing affects reproductive output and thus

recruitment. As Caddy and Gulland (1983) noted, fish stocks in steady state are common in textbooks but rare in the marine environment. Weakfish have demonstrated large fluctuations in year-class strength (Mercer 1985, Vaughan et al. 1991, Chapter 2) and thus the assumption of constant recruitment and natural mortality—necessary for yield per recruit analysis—is not met. Such a stock can still be assessed by standard methods, but there will be more uncertainty associated with the results. The uncertainty can be decreased if the causes of the natural variation are understood (Caddy and Gulland 1983).

Thus, it is important that the historic pattern of weakfish landings be taken into consideration. Coastwide weakfish landings have shown three peaks over the past century, one in the early 1900's, a second during the 1930's/1940's and a third in the late 1970's/early 1980's. The lowest period of weakfish landings occurred during a 20-year-period in the 1950's and 1960's. The duration of which appears too long to be due to random negative environmental factors. Two hypotheses for these low weakfish landings were developed: recruitment overfishing during the 1930's and 1940's (Perlmutter et al. 1956, Perlmutter 1959, Joseph 1972, Merriner 1973) and/or reproductive failure due to estuarine pollution (Joseph 1972). Both assume a decrease in recruitment, and thus stock size, due to decreased weakfish reproduction.

However, the weakfish reproductive pattern of early maturation, multiple spawns over an extended spawning period, and high fecundity (Chapter 3)—suggests weakfish would not be very susceptible to recruitment overfishing. Nevertheless, the potential in weakfish for large fluctuations in annual population fecundity due to factors other than F (Chapter 3) suggests the same level of fishing could effect weakfish reproductive output differently in different years. It also suggests weakfish stock abundance may fluctuate naturally.

In conclusion, yield-per-recruit analysis presented here must be evaluated in conjunction with the historic pattern of weakfish landings and the acknowledgement that the relationship between fishing and weakfish reproduction is not yet well-understood. Year-class strength affects weakfish landings and varies for reasons other than F and t_c. Because of this, weakfish management strategies should recognize that the peak in landings in the early 1980's may have been an extreme due to a run of strong year-classes. This peak should not be considered the normal abundance and age structure of the stock under rates of heavy exploitation. Similarly, although weakfish are clearly being fished before they have been given a chance to grow to an optimal size, the decreased landings since the early 1980's may be due to decreased year-class strength as much as over-exploitation. Thus, it will be necessary to better

understand what causes fluctuations in weakfish landings, as well as how weakfish interact with other species, before a comprehensive management strategy can be developed.

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